VARIATION IN THE WESTERN ZOSTEROPIDAE (AVES)

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PART 1

INTRODUCTION

The Zosteropidae (White-eyes) are a tropical passerine family, with a range over the whole of the Ethiopian Region and eastwards, through the islands of the Indian Ocean and India to Japan, the central Pacific and Australasia. There is, however, a gap of over a thousand miles, presumably imposed by ecological conditions, between about 50° E. and 66° E., across eastern Arabia, Persia and Baluchistan.

The family is for the most part very homogeneous, and has long been recognized as presenting special difficulties for the taxonomist. Stresemann (1931, 1939) has reviewed the populations from India eastwards, comprising about 180 forms, most of which are unquestionably to be placed in the genus *Zosterops*. For the remaining Zosteropidae, those of Africa and the Indian Ocean, no conspectus is available except the list incidental to the *Systema Avium Aethiopicarum* of Sclater (1930). He provisionally accepted 57 forms in the area and grouped them in 18 species of *Zosterops* (10 of them monotypic), 4 monotypic species of *Speirops* and 3 of *Malacirops*. In footnotes he mentioned 15 forms as probable synonyms ; and since he wrote 15 more forms have been described. More recently van Someren (1939), Grant and Mackworth-Praed (1943) and Mackworth-Praed and Grant (1945–46) have reviewed sections of the African continental birds, Bannerman (1948) has dealt incidentally with the West African forms, and Chapin (1954) with those found in the Belgian Congo. Between the various authors named there is great diversity of opinion about the number of forms that should be recognized and about their grouping into species. For example, of the 11 forms common to the discussions of both Chapin and Grant & Mackworth-Praed, Chapin admitted 4 that the other authors synonymized and differed from them about the specific allocation of 3 others. Agreement on local variation (at the subspecific level) is made more difficult because, as I believe, changes are liable to take place in the yellows and greens of *Zosterops* skins in a short time (see examples in Note 1 of Appendix 1). It may be added that most of the information about the biology of Zosteropidae is merely casual and incidental.

This study began as an attempt to revise the classification of the African Zosteropidae but as the work progressed I became increasingly impressed with the problems of their variation (as distinct from nomenclature) and their correlation with environmental factors. The opportunities for investigating these correlations are particularly good because Africa is so mountainous and otherwise provides so great a variety of habitats through which the *Zosterops* range.

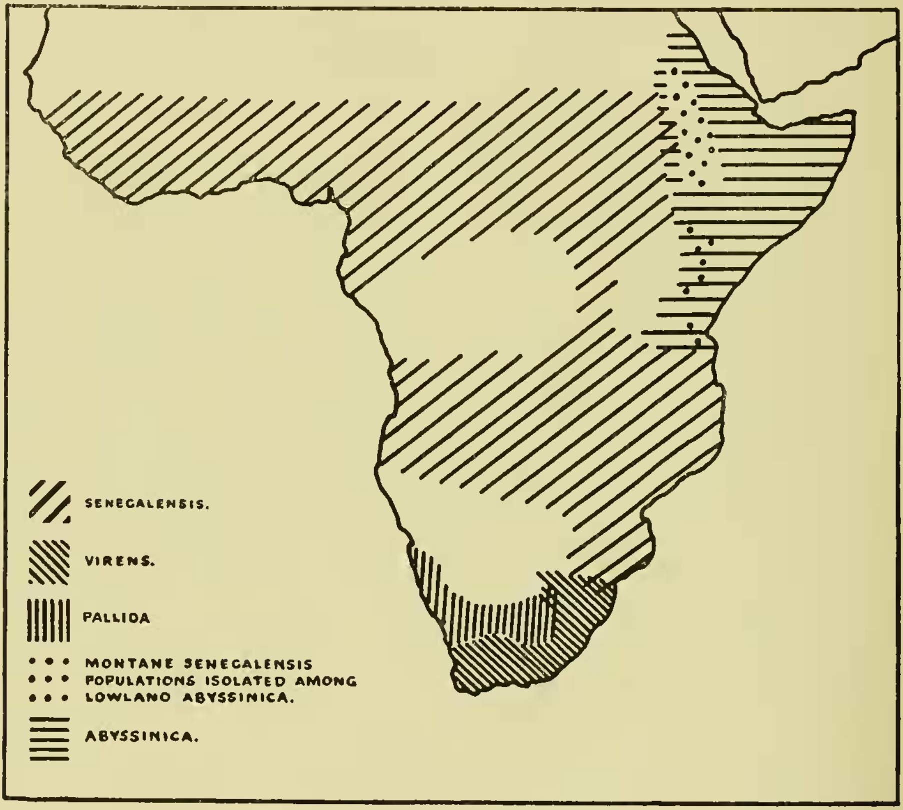
Taxonomically, the great difficulty in this family is to determine the limits of the species. The *Zosterops* of Africa have more than once been cited as providing special problems when the concepts of allopatry and sympatry are applied. Lowland forms surround highland forms in such a way that their geographical ranges overlap in some cases completely, but their ecological ranges little if at all. In such cases the spatial barrier is, at most, of the smallest, a matter of a few hundred yards, and cases (detailed in the appropriate sections below) have come to light in which, at least locally and temporarily, none exists. How far the breeding-seasons of the highland and lowland forms overlap in any one locality is unfortunately not known for any except the special case of Nyasaland (where they do—Benson, 1953). But on the whole it appears that where two *Zosterops* occur in Africa in the same small area, while they may be " genetically sympatric " (Cain, 1954) only marginally, they cannot be regarded as " genetically allopatric " to such an extent as to exclude the possibility of frequent interbreeding. In such circumstances, the absence or rarity of hybrids, whether of the primary type (evenly intergrading) or the secondary type (widely and sporadically variable), can be taken to mean that the forms concerned are genetically so incompatible that they are best treated as belonging to different species.

The subject of the present study is difficult to expound, partly because of the unavoidable amount of geographical and other detail, but also because of the difficulties inseparable from the use of trinomial nomenclature, which have been discussed by several recent workers (for example, Lack, 1946 ; Ellerman *et al.*, 1953 ; Wilson and Brown, 1953 ; Sibley, 1954). Nobody dealing with a large body of material from a continental area can fail to be impressed by the virtual impossibility of allocating every population, let alone every specimen, to a recognizable subspecies ; and if one is forced to attempt it for purposes of a check list it can only be at the cost of obscuring biological realities. An excellent example from the area under review is provided by the *Zosterops* of Madagascar. Originally they were treated as all belonging to one form ; now the palest birds and the largest birds have been separately named, though it has to be conceded that most of the *Zosterops* on the island are intermediate between the three subspecific types. I personally am deeply impressed not only with the shortcomings of the trinomial system but also by the harm that has been done to ornithology by the extremes to which the naming of local populations has been carried. Nevertheless, I regard the retention of some trinomials as essential, at least as a clerical convenience, especially when dealing with birds of a continental area. This is the spirit in which the trinomial is used in the present study.

In the pages that follow I shall first discuss the probable taxonomic significance of colour, which has hitherto been the sole character on which the specific classification of the Zosteropidae of Africa and the neighbouring islands has been based, and then the correlations of dimensions with each other and with environmental factors. This will bring into prominence certain basic principles, will show the extent of local variation and adaptation, and will lead to the conclusion that here dimensional characters can be only exceptionally and to a minor extent an aid to classification.

As regards classification at the specific level, I believe that reliance on colour characters has led to misleading results in the past ; and that some of the birds which differ conspicuously to the eye are more closely related than some of those which are most alike. In several islands on both sides of Africa two fully sympatric species of Zosteropidae occur—doubtless as a result of double invasion. By contrast, throughout the continent of Africa there are only two places, the upper slopes of

Cameroon Mt. and the south-western Transvaal, where two different forms are fully sympatric. In a third area, Zululand and its neighbourhood, two forms interdigitate, separated ecologically and apparently interbreeding little, while throughout north-eastern Africa a series of lowland forms, which I believe to form one polytypic species, surrounds a galaxy of isolated and well-differentiated montane populations. Besides the aberrant bird on the top of Cameroon Mt. which I keep in the genus



MAP 1. The ranges of *Zosterops* species.

Speirops (see discussion in Part 5) I provisionally group the African *Zosterops* as shown in Map 1:

- *Z. pallida*, monotypic in south-western Africa and overlapping—
- *Z. virens*, occupying the rest of South Africa and interdigitating with—
- *Z. senegalensis*, a highly polytypic species occupying most of tropical Africa and becoming purely montane in the northeast, where it is surrounded by—
- *Z. abyssinica*, a polytypic species characteristic of the dry lowlands.

These conclusions depend on a number of decisions that are by no means easy to take and the evidence needs to be set out in some detail (Part 4).

Following the description of the continental position, the insular populations on the opposite sides of Africa will be described. One special point of interest here is the evidence for double invasion, into one island after another, the evolutionary consequences of which can be fully appreciated only in the light of the continental situation. Further, the lines on which evolution has taken place in the Atlantic islands (Gulf of Guinea) have differed strikingly from those in the Indian Ocean Islands.

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SOME CHARACTERS OF THE ZOSTEROPIDAE AND OF THE AFRICAN MEMBERS

In appearance the Zosteropidae are rather " ordinary " passerines nearly all less than 14 cm. long. The size range is not great ; omitting two aberrant insular forms usually kept in the genus *Speirops*, within the present area the following are the extreme measurements : wings 49–69 mm., tails 30–53, beaks 11–17. Morphological characteristics of the family are absence or extreme reduction of the outermost primary, a fimbriated bifid tongue and a ring of silky-white feathers round the eye. The Zosteropidae are all short-winged birds, of direct flight, and thoroughly arboreal habits. The beak is rather sharp and slightly decurved.

Certain behaviour-characters of the family are significant in any consideration of their evolution :

(1) The birds have a wide range of food, taking fruit, insects and nectar, and in this respect there seems to be no specialization, local or other. Their feeding habits often bring them into association with sunbirds, alongside which they are always placed in taxonomic order.

(2) Individuals of most forms have a strong tendency to flock. Consequently birds journeying outside their normal area are likely to do so in groups and successful colonization is thus facilitated.

(3) White-eyes are liable to erupt and cross several hundred miles of sea. They have colonized more oceanic islands than any other passerine genus. That the Australian *Z. lateralis* invaded New Zealand across more than 1,000 miles of sea is a matter of history ; and that Norfolk Island, some 500 miles from any other *Zosterops* station, has been successfully colonized three times is certain from its three different forms of *Zosterops*.

(4) In conflict with this, the presence of highly differentiated populations on both marine islands and continental mountains within sight of each other seems evidence that the birds of some populations must be profoundly sedentary. An extreme instance is that of the *Z. rendovae* group (cf. Mayr 1947), where water-gaps of less than two miles separate subspecies.

Especially in a continental area, such as Africa, the birds would be expected to be most sedentary in the most equable environment (evergreen conditions) and least sedentary where the seasonal changes are greatest. There is good indirect evidence of this :

(*a*) A series of populations (52–54 in Appendix 3) having identical plumage and living in an evergreen-forest climate on the eastern rim of the Congo basin has average wing-length 61·3 mm. at 7,000 ft., 55·9 mm. forty miles to the west, at 4,300 ft., and 53·1 mm. twenty miles west again, at 3,000 ft.

(*b*) In East Africa very distinct populations live on forested mountains, separated from each other by as little as twenty miles.

(*c*) By contrast, the *Zosterops* ranging through the belt of deciduous thorn-bush south of the Sahara has not differentiated to the subspecific level in the three thousand miles from Senegal to the eastern Sudan.

There is little direct evidence of movement : the most definite is that the *Zosterops* characteristic of the very dry country of southern South West Africa sometimes appear for a few days in Windhoek (W. Hoesch *in litt.*), some 150 miles from where birds of this kind are known to be resident.

Birds usually assigned to the genus *Zosterops* comprise more than four-fifths of the Zosteropidae. Nearly all of these have the upper parts more or less green—

with a range of colour from dull pale grey-green to bright yellow-green and rich olive-green ; their throats and vents are more or less yellow. They have no distinctive patterns on wings or tails and no spots or speckles anywhere. There is no sexual dimorphism except that females tend to be a little smaller and, like juveniles, a little duller in plumage (having less carotenoid). Individual variation is, however, high—so much so that I should expect the results obtained by Marples (1945) to find a parallel in African populations if comparable series were examined. He was able to classify the belly-colour of *Z. lateralis*, trapped at Dunedin, New Zealand, in winter into nine different categories.

Apart from differences in shade and in dimensions, the main variations between populations are in three features :

(1) The width of the ring of white feathers round the eye (a feature that unfortunately does not lend itself to accurate measurement). Since an eye-ring exists in the vast majority of the Zosteropidae, and often is retained in aberrant forms whose other characters are much modified, it might be supposed to be of biological importance. But there is no evidence of its function, whether in display or in any other way, and within Africa it varies in extent from a conspicuous white patch, covering half the side of the head, to an almost imperceptible rim round the eye. Moreover it is sometimes altogether lost in otherwise "normal" *Zosterops*. On the whole it cannot be regarded as diagnostically useful except at the subspecific level.

(2) Markings on the forepart of the head. These are usually limited to lines above the lores and/or areas on the forehead where the melanin is reduced, so that they appear more yellow than the rest of the upper parts. If these brighter areas were sharply demarcated, they would be more comparable for taxonomic purposes.

(3) The underparts between the upper breast and the under tail-coverts. These are nearly always either yellow, with some green wash, especially on the flanks, or whitish washed with greyish or brownish. This feature is discussed specially in Part 2.

Particularly within the Zosteropidae discussed in this paper, there are extremely few clear-cut differences in pattern. Nearly all those perceptible between populations are merely a matter of degree—nuances of intensity of melanin or carotenoid ; while the one striking difference in pattern in the continental African birds, yellow or no yellow on the belly, which has been accepted as a specific difference, cannot be regarded as a reliable guide to relationships, as shown in Part 2.

Since the genus *Zosterops* includes over 200 recognized forms and for the most part varies only within the narrow limits indicated above, it is easy for widely separated populations to show resemblances that must be the result of convergent evolution rather than of close affinity ; and the systematist's task is correspondingly more difficult. For example Madagascar *Zosterops* are very like those of New Guinea (among others), those of the Australian mangroves (*lutea*) like those of the East African lowlands (*flavilateralis*), and those of Annobon Island in the Gulf of Guinea (*griseovirescens*) like those of Christmas Island in the Indian Ocean (*natalis*). Again, within our area, Madagascar *Zosterops* differ from those of south-western Abyssinia only in lacking golden foreheads and in having a little more melanin generally (characters that are not independent). Moreover, this difference is comparable to that (also confined to colour) between *Zosterops* from Madagascar and from India ; for, while most of the latter are much yellower than the former, Nilgiri birds are intermediate. Again, within Africa itself, some *Zosterops*, separated by hundreds of miles occupied by other forms, are indistinguishable, such as those of the mountains on the Sudan–Uganda border and some of those in Tanganyika Territory.

In such circumstances, where the appearance of the birds can be so unsafe a guide to their affinities, as many ancillary characters as possible must be considered. Among the most important of these is habitat preference. In his study of the eastern Zosteropidae Stresemann (1931) regarded their ecology (particularly their preference for lowland and highland habitats respectively) as an important guide to their relationships at the specific level. (Yet he was forced to postulate considerable change in ecological preferences in arriving at his grouping of forms into the polytypic *Z. citrinella* and still more in his enlarged concept of *Z. palpebrosa* (Stresemann, 1939)). There is no doubt that for African birds in general habitat preferences are highly specific, and in some cases generic, especially as between forest and non-forest and between highland and lowland habitats (cf. the analysis in Moreau, 1954). Unfortunately in the African *Zosterops* these distinctions and preferences are less clear-cut.

This is presumably due in part to their way of life : they are not ground-feeding birds, which in evergreen forests are immersed in a specialized eco-climate, nor forest-canopy birds, which may be limited by the distribution of certain species of fruiting trees or of tree-holes. Instead, the *Zosterops* have a wide range of diet and no specialized nesting-site ; moreover those forms which are attracted to evergreen forest appear to belong to the edges rather than the depths. (There is no *Zosterops* at all in the main Congo forest area, even in the clearings.) Also, most forms of *Zosterops*, including those of evergreen forest, seem to adapt themselves readily to whatever man-made conditions provide trees and associated food. Even those *Zosterops* which are always cited as forest birds, such as those in the southern Cameroons and on the East African mountains, may perhaps be looked upon as birds that use the arboreal associations dominating the locality rather than birds ineluctably dependent on forest, as most members of the evergreen-forest communities seem to be. If this view is correct, then different populations of the same species of *Zosterops* may be found occupying in one part of Africa savanna trees or even thorn-bush, and in others evergreen forest, with more or less ecotypical modification of characters. As will be pointed out, this is what happens in Madagascar, where *Zosterops* unquestionably of the same species occupy all types of vegetation and climate from the " subdesert " of the south-west to the east coast with over 100 inches of rain. Again, in South Africa birds that cannot be separated taxonomically are found breeding in a range of climate and natural vegetation from the coast of the Indian Ocean and associated evergreen forests, to the " high-veldt " of the Transvaal with its far greater daily and annual range of temperature and far drier and more deciduous " bush ". This is not to deny that such birds as the montane *kikuyuensis* of the eastern Kenya highlands and the lowland *flavilateralis* are usually separated ecologically—even though in a marginal locality, such as near Nairobi, they may frequent the same garden. But it is at least clear that, in the key problem of which forms of the African *Zosterops* should be allocated to which species, in cases of difficulty the habitat preferences are not sure guides.

Other ancillary characters which have been considered are (1) colour of beak, iris and legs, (2) form of beak and tongue, (3) wing-formula, (4) voice, (5) feathering sequence of nestling. Certain of these, especially (2) are probably particularly adaptive and labile, but in any event, on examination, none of them seems to be capable of giving important clues in difficult cases. Details are therefore relegated to Appendix 2. Only two points in connection with them need be noted here :

(*a*) Such differences in wing-formula as exist seem to have neither taxonomic nor consistent ecological relationships. Two of the forms with the bluntest wings belong to dry country, but in two others of equally dry country (with open thorny trees) the character is not so marked ; and on other grounds there is little doubt that the four forms belong to at least three different species.

(*b*) Beaks and tongues are much alike in all the continental African and nearly all the insular birds under consideration, irrespective of habitat.

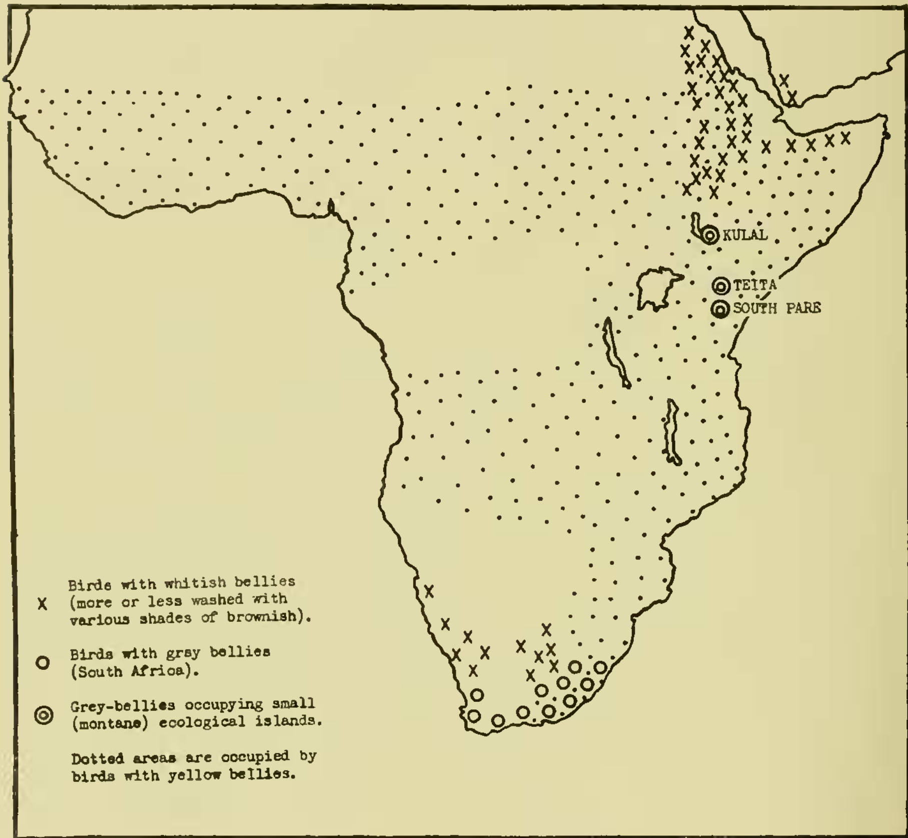
(*c*) The songs of some of the most different-looking African *Zosterops*, which have usually been allocated to different species, are apparently alike.

In attempting to discuss relationships and evolution one further difficulty is encountered, namely, apart from certain details of the plumage (see Part 2), there is no sure indication in the Zosteropidae of which features are the most readily modified. For example, *albogularis* of Norfolk Island has attained giant stature while retaining the presumed ancestral colouring, including full carotenoid and white eye-ring. Yet in a few forms the eye-ring seems to have been one of the first characters to be reduced or lost (at the subspecific level in *uropygialis* of one of the Kei Islands). On the other hand, one of the Seychelles birds, *modesta*, has lost all its yellow pigment, and become uniform grey, without becoming abnormal in size, proportions, beak or eye-ring. In the insular Zosteropidae, in fact, it seems that a rather limited variety of evolutionary changes can take place, with one exception, in almost any order.

PART 2

COLOUR, PATTERN, PIGMENT AND ENVIRONMENT

As indicated in Part 1, the most prominent colour differences between forms of Zosteropidae is that some have yellow pigment (more or less washed with green) on the belly and some do not. Stresemann (1931) noted in discussing the Indo-Pacific Zosteropidae that absence of yellow from the belly is much commoner than its absence from either the throat or the under tail-coverts. In fact, this last occurs only if yellow pigment is lacking from the whole of the rest of the underparts—which usually means from the upper parts as well. These generalizations apply equally to the African and insular Zosteropidae dealt with in the present study. It may be noted also that absence of yellow from the belly is unknown as an individual abnormality in a yellow-bellied population, though absence or reduction of carotenoid



Map 2. The geographical distribution of *Zosterops* belly-colour.

from the whole plumage occurs, as well as loss from defined asymmetrical patches (see Note 2, Appendix 1).

All who have dealt with the taxonomy of the African *Zosterops* have regarded the populations that have yellow bellies as specifically distinct from those which have not, though there has been no agreement about how many species of either type should be recognized. By contrast, however, in a number of polytypic Indo-Pacific

Zosterops species Stresemann (1931) and Mayr (1944) include both populations with yellow on the belly and populations without. Stresemann concluded that the difference probably depends on a single genetical factor. This must be true in any case where the two types co-exist and are proved to interbreed without producing any birds of intermediate plumage, but this condition does not seem to have been completely satisfied anywhere and at least in Java the evidence is against a single-factor explanation (Mees, 1951 ; Note 3, Appendix 1). There is in the island a complete range of variation between the yellow-bellied *gallio* and the grey-bellied *buxtoni* ; and it is instructive to note that many of the specimens are so like one of the parents that they would have escaped detection as hybrids if they had been seen in isolation.

In Africa what has been discovered in recent years about the relationship between the two types of *Zosterops* makes it virtually certain that here also belly-colour is not a specific character. For one thing, the grey-bellies occur only in widely separated areas (Map 2), isolated from each other by yellow-bellied populations that occupy equivalent niches in the intervening country (for details of distribution see Part 4).

The grey-belly locations fall into three groups :

North-east Africa.

In the Abyssinian highlands grey-bellied *poliogastra* and yellow-bellied *kaffensis* are almost allopatric and no intermediates are known.

The lowlands are occupied by grey-bellied birds (*abyssinica* and *omoensis*) except in the west-centre and the south-east. They are allopatric to yellow-bellied birds except near Lake Tana.

Kenya and Tanganyika Territory.

Here the numerous isolated mountains form an ecological archipelago. Grey-bellied *Zosterops* occupy exclusively (1) Kulal Mt. (*kulalensis*), (2) the Teita group (*silvana*), (3) the South Pare range (*winifredae*). The intervening and other mountains are occupied exclusively by various forms of yellow-bellied *Zosterops*, and each of the three grey-bellies is more like its nearest montane yellow-belly neighbour than any other.

South Africa.

In the Cape Province grey-bellies predominate in the west, yellow-bellies (otherwise identical) in the east. They overlap considerably and in the middle they are proved to interbreed commonly. Unfortunately the data do not suffice to settle the genetics.

Another form lacking yellow on the belly occupies South West Africa and overlaps the yellow-belly marginally, but in this case there is no evidence of interbreeding.

The foregoing data, taken as a whole, certainly suggest that in Africa colour of belly is a character with a simple genetical basis and that grey-bellied populations have developed repeatedly. In East Africa the montane grey-bellied forms have every appearance of having arisen as so many different mutants from the neighbouring yellow-bellies. It is concluded that in the *Zosterops* of Africa, as in those of the East, belly-colour is not necessarily a specific character. There is nothing to indicate how the present geographical pattern arose. It is difficult to believe that the character "grey-belly" is directly adaptive and, even with personal knowledge of East African mountains, I cannot suggest what factors can have operated particularly on Kulal, Teita and South Pare to select any characters with which "grey-belly" might be linked. It may be added that, though probably the Kulal and Teita birds are hardly to be numbered in thousands, the populations are far too big for the Sewall-Wright effect to be accepted as bringing about the present situation.

Much of the taxonomic discussion about the African continental Zosteropidae has turned upon the exact shade of yellowish green or greenish yellow of the upper parts, and the amount of green on the sides of yellow underparts. The colour intensity of the blackish lores and of the remiges and rectrices has also been adduced as a character. These are, however, not independent features because they are all correlated with the nature of the melanin present in the plumage as a whole and with the degree of its concentration. If much melanin is present in the upper parts, the yellow on the front of the head is, as a rule, less than in closely similar populations that have the upper parts as a whole not so dark. Conversely, the amount of greenish wash on the flanks generally varies with the darkness of the upper parts.

The physical basis of the coloration of the Zosteropidae does not seem to have been described anywhere and I am greatly indebted to Dr. L. Auber of the Wool Industries Research Station at Leeds for making microscopical investigations for me. It is hoped to extend and publish the results separately. Dr. Auber finds that in *Zosterops* pigments of only two groups are present, carotenoid (yellow) and melanin (three types). In the terminal (exposed) part of each contour feather the barb and/or the individual barbules have more or less of their length yellow and the rest melanic. Superimposed on each other in the plumage, they give, by a "lattice" effect, green. The exact shade depends on (*a*) the relative extension of the yellow and the melanized parts of each barbule, (*b*) the shade of each of the pigments, (*c*) their concentration and distribution within the tissue.[1] This last is especially important with the carotenoid, for the intensity of the yellow colour depends mainly on the thickness of the layer containing the pigment. This is especially important in the barbs, where the thicker the cortex (the layer holding the carotenoid) the more intense the yellow, towards golden or even orange. This effect appears to be mainly responsible for the striking difference between the pale yellow on the forehead of *abyssinica* and the strong reddish-golden of the Kenya *kikuyuensis*. In the former the unpigmented central core (medulla) of the barbs is wide, while in the latter it is so reduced that the barb forms practically a column saturated with carotenoid. Here, then, is a case in which the colour depends on the anatomy of the feather as well as on the pigment.

[1] The conventional phrase "grey wash" or "green wash" is misleading in so far as it implies a pigment applied externally. In the *Zosterops* an impression of "grey wash" is given in an area of plumage that contains some melanin but little or no yellow pigment, and of "green wash" by an increase in melanization in the presence of yellow pigment.

With the melanins the optical effect depends largely, but by no means wholly, on the type of melanization. In approximate agreement with the observations of Görnitz (1923) and Frank (1939) on other groups of birds, Dr. Auber distinguishes three types of melanization in the African *Zosterops*, namely :

(A) Rodlets more than 1μ long, coated with blackish pigment and arranged with their axes parallel to the main axis of the barbule.

(B) Granules shorter and more irregular than (A) and which under the microscope look more brownish.

(C) Very small irregular granules, bright reddish brown. This type is rarer than the others in the African *Zosterops* ; it predominates (and causes a reddish colouring) only in the flank-feathers of the dry-country birds of south-western Africa (*pallida*) and in two insular birds (*semiflava* and *mayottensis*) living in a much damper oceanic climate.

Throughout Africa the melanin in the plumage of each form of *Zosterops* is predominantly or (usually) exclusively, of either (A) type or (B) type. Since the second pigment is much browner than the first it might be supposed that the type of melanization would proclaim itself to the eye but, for reasons not altogether clear, this is not always so. The outstanding example of this is afforded by the abnormal birds of the Gulf of Guinea islands, which are browner than any other Zosteropidae, yet contain much (A) type melanin. Again, the dry-country birds of rather dingy appearance in both north-east and south-west Africa, *abyssinica* and *pallida*, are dominated by (B) type, while the *Zosterops* of the humid São Tomé and Principe Islands, the upper parts of which look very similar, are filled with (A) type. Also, while in all the richer green *Zosterops* of Africa (A)-type melanization predominates, the Cape bird, which looks similar, is mainly (B) ; and such melanin as exists in the brightest yellow *Zosterops* in Africa, *senegalensis* of the dry belt south of the Sahara and *anderssoni* of the Rhodesias, is entirely (A). Incidentally, this explains the full blackness of the loral spot in these latter birds, a feature at first sight surprising in a *Zosterops* whose general plumage gives so little sign of black pigment.

In certain South African forms the proportion of (A) and (B) melanization in the individual varies with the humidity of the environment. Dr. Auber has found that in the birds of the western Cape Province (*capensis*) the admixture of (A) in the predominant (B) is greater in the humid Knysna area than in the arid Kamiesburg. Also, in *virens* of eastern South Africa the melanization is chiefly (A) in the humid Natal highlands, (B) in a dry-veldt habitat in the Transvaal. By contrast, *senegalensis* has all its melanin of (A) type, even in the driest environment (cf. a specimen from Maiduguri, near Lake Chad). This presumably means either that there is a different (undetected) environmental factor operating or, more probably, that *senegalensis* is physiologically (genetically) different from these South African birds and also from the other dry-country *Zosterops* (of north-eastern Africa), which are characterized by (B) melanin.

On the whole, as will be seen from the descriptions in Part 4, the more richly green birds throughout Africa occur in the more humid areas and this is everywhere linked—by whatever mechanism—with a greater intensity of (A) melanization in the plumage. There are very strong indications that the change takes place clinally in step with change in vegetation-type. The change is less closely correlated with total annual rainfall because other climatic factors, such as seasonal cloud-cover, extent of occult precipitation, and above all distribution of rainfall through the year, all determine the biological effectiveness of the rain. Thus, less than 60 inches of rain can suffice for evergreen forest if there is no long dry season, but not otherwise.

From all of the foregoing it will be evident that on the whole the African *Zosterops* conform to Gloger's rule, under which, as summarized by Mayr (1947), melanins increase in the warmer and more humid climates and in arid climates reddish- or yellowish-brown melanins increase at the expense of black. But in the African *Zosterops* it appears that melanins increase in the warmer climates only where the humidity is not reduced; and, so far as the type of melanin is concerned, the exclusive presence of black in the dry-country *senegalensis* is an exception to Gloger's rule.

To summarize this section, it appears that belly-colour cannot in these *Zosterops* be taken as a guide to taxonomic affinities, nor can general plumage-colour nor, as a rule, the type of melanization present—which often does not proclaim itself to the eye.

PART 3

DIMENSIONS AND THEIR CORRELATIONS IN CONTINENTAL *ZOSTEROPS*

The inquiry into these correlations was started in the hope of finding peculiarities and discontinuities that might help to elucidate the taxonomy of the birds. This section has taken its present form thanks to the statistical analysis arranged for by Mr. N. J. T. Bailey in his department of Design and Analysis of Scientific Experiment, at Oxford; and what follows here owes a great deal to discussions with him, with Mr. John Barlee and with Dr. H. W. Parker, who has devoted much time to the problems here raised.

The variations investigated are those of wing-length, tail-length and beak-length in relation to temperature and altitude, and in relation to each other. Investigation of these environmental effects is complicated by the fact that temperatures vary with altitude. Diverse as the temperatures are in different parts of Africa at the same altitude, in any given locality the temperature falls by about 3·5° F. for every 1,000-foot rise in altitude. The other factor that changes consistently with altitude, air-pressure, falls off by about 2·5%[1] of sea-level pressure for every 1,000 ft. of altitude and is not subject to important local variations.

By a suitable statistical technique the relations of dimensions to environmental temperature can be separated from altitude effects and considered independently, with special references to Bergmann's rule. As summarized by Mayr (1947), this

[1] This figure is net, taking account of the effect that the reduction in temperature has on the air-pressure. I am indebted to Dr. Parker for pointing out also that air-density is affected by humidity, being reduced as humidity increases; but the effect is small enough to be ignored for the present purpose.

is to the effect that "smaller geographic races of a species are found in the warmer parts of the range, the larger-sized races in the cooler". Under "Rules applying to birds only" it is also stated that "the wings of races that live in a cold climate or in the high mountains are relatively longer than those of the races which live in the lowlands or in a warm climate". It is not clear whether the word "relatively" means "relative to body-size"; if it does, then it must be noted that none of the references quoted by Mayr in support of this statement provide conclusive evidence.

Comparisons for this purpose have usually been made in the broadest terms, using latitude as an indicator of temperature, rather than actual meteorological data, and without discussing which elements of the environmental temperature are the most significant. It might be expected, *a priori*, that selection would be exercised by the more extreme conditions encountered; Huxley (1942) in fact suggested that in the temperate zones these would be primarily the winter minima and in the sub-tropics (presumably even more in the tropics) the summer maxima.

The term used in the formulation of Bergmann's rule is "size", which presumably means the size of the animal as a whole; and consideration of the relations between size and temperature turns ultimately on the fact that, other things being equal, the heat exchange between a body and its environment depends on the ratio between its volume and its surface. The bigger and/or the more compact the body, the less rapid (per unit of mass) its heat-exchange. The bigger the body, the better it is fitted to withstand cold; and the smaller the body the more easily it can, through radiation and evaporation, lose heat.

For vertebrates, weight is a useful indicator of size, but for most birds so little is known about the weight that in ornithology wing-length is almost always used as an index of body-size, with the tacit assumption that the relationship is linear. (Incidentally, the standard measurement of wing-length is not skeletal, but effectively that of the longest feather.) Now, if the shape of the wing and all the other bodily proportions remain constant, the "lift" provided by the wing varies as the square of the wing-length, while the mass of the whole bird varies as the cube. In these circumstances, if efficacy of flight is to be maintained it can be by an improvement in flying technique or by the length of the wing increasing faster than the linear dimensions of other parts of the body. In this case wing-length, so far from bearing a linear relation to the mass of a bird, would bear a complex and also continually changing relation to it, and hence to the bird's potentiality for heat-exchange.

Since no weights are recorded for African *Zosterops*, no data exist for testing the ratio of wing-length to mass in any of the populations[1], so that a link essential for any comprehensive discussion of size/temperature relationships is missing. Two further caveats are needed. The first is that the African *Zosterops* cannot all be claimed to belong to one species, which is a condition of Bergmann's rule; but, as will be concluded, most of them appear to be conspecific. The other caveat is that

[1] An investigation of the mean weight of bird populations for statistical purposes such as the present would need especially long and critically collected series because the weight of the individual fluctuates so much with the time of day and season of the year. In *Zosterops* at Dunedin, N.Z., Marples (1945) found that *mean* weights of samples trapped on different days in the course of the year varied between 12 and 15 gm.

heat-exchange depends on insulation as well as on mass and configuration ; we have no precise information on this point. It can only be said that the *Zosterops* of the higher, cooler, environments appear to have thicker plumage than the others.

The dimensional data

For the present study about 2,500 specimens have been measured, a large proportion of all those housed in the museums of the world. As will be seen from Appendix 3, there are eighty continental populations of which enough specimens have been examined to give results useful for statistical treatment. Some of these " populations " coincide with named forms, but many of them do not. The latter are of three types : (*a*) geographical sections of forms with very extensive ranges, for example the respective Northern Rhodesian, Southern Rhodesian, Nyasaland and S.W. Belgian Congo populations of *anderssoni* ; (*b*) altitudinal divisions, as between the *Zosterops* of the eastern Kenya highlands above and below 9,500 ft ; (*c*) populations that are transitional and/or were not known to earlier workers (so that no subspecific name has been applied to them in the past). Other specimens and their dimensions are mentioned in the text as necessary.

All the measurements given in Appendix 3 were made by me personally, so that any subjective error should be fairly constant. Wings have been flattened and straightened, so that the measurement recorded is the greatest possible. Tails have been measured with one point of the dividers pressed down between the two middle feathers. Beak measurements are particularly difficult in *Zosterops* because of the lack of abruptness in transition from culmen to skull. At first, indeed, I felt that this measurement could not usefully be made, but eventually I found that fairly satisfactory results were possible—cf. the length-ranges in Appendix 3. In each case the point of the dividers was slid with gentle pressure up beyond the base of the culmen until it was decisively checked.

In the entire series of continental birds examined wing-length varies from 49 to 69 mm. in individuals and from 51·3 to 64 mm. in means. Extreme variation within populations is nearly always 4–7 mm., i.e. up to about 12% of the mean. The few populations in which it is much greater are either represented by exceptionally long series or could possibly be sub-divided if more specimens, suitably distributed geographically or altitudinally, were available. An example is provided in the highlands west of Lake Edward (populations 48 and 49 in Appendix 3). The specimens at first examined showed within this small area wing-lengths with the exceptional range of 54–65 mm. Later it was found that 31 birds from an average altitude of 4,700 ft. (the highest 5,000 ft.) measured 54–60 mm. and 10 from an average altitude of 6,800 ft. 58–65 mm. In general, individual variation in tail-lengths and beak-lengths is proportionately greater than in wing-lengths, perhaps partly because of the greater difficulty in making the measurements.

A small source of bias in the figures for the means comes from the fact that males, females and unsexed birds have all been used, provided that they showed no immaturity and no moult in the feathers to be measured. It would have been more satisfactory to use birds of only one sex, but this was rejected for two reasons. Firstly, the sexing of collected specimens is not always reliable and in some populations specimens that are not sexed form a large part of the material available. Secondly, although females are on the average smaller than males in most populations, the difference does not exceed 2 mm. in even the biggest *Zosterops*. Moreover, in nearly all the populations the proportion of sexed female specimens varies only between one quarter and one half of the total, and within these limits the most the mean could be biassed by this variable is about 0·5 mm. This is not enough to invalidate the general conclusions to be drawn later.

The meteorological data

For each population in Appendix 3 a mean altitude has been calculated for the specimens actually measured. (This mean does not necessarily agree with the mean altitude of the habitat of the *Zosterops* population concerned over its whole range.) Where no altitude is specified on the label of a specimen it has been estimated from its locality and such knowledge of the topography as could be obtained. It is thought that most of the mean altitudes given in Appendix 3 are accurate to within 500 ft.

These mean altitudes have been used as the datum-lines for calculating the temperatures that are given for each population in Appendix 3, namely, the mean minimum of the three coldest months and the mean maximum of the three hottest. (From these figures approximate annual means and annual ranges can be calculated as needed.) Thanks to the assistance of the Meteorological Office, Air Ministry, and supplementary information from African meteorological services, temperature data have been assembled for about 1,000 stations south of the Sahara. Within the geographical range of most of the populations in Appendix 3 a number of temperature records are available, some of the stations being as a rule higher and some lower than the mean altitude of the specimens concerned. From these records mean temperatures have been calculated and also the mean altitude of the stations. Where this differs from the mean altitude of the specimens available an adjustment has been made at the rate of 3·5° F. per 1,000 ft. Extrapolation has been used in two types of case :

(*a*) Where, as in birds from high altitudes in eastern Kenya and Mt. Cameroon, mean altitude of the specimens is thousands of feet above that of the local meteorological stations, the same factor of 3·5° F. per 1,000 ft. has been used.

(*b*) Where, as in the case of populations very narrowly localized, e.g. on single isolated peaks, meteorological stations are available only elsewhere in the same general area, a mean has been calculated from the data of the nearest ecologically comparable stations (and then the altitude correction applied if necessary).

Especially in the latter type of case, unknown local meteorological factors may invalidate to some extent such extrapolation, as personal experience of East Africa suggests, and for two of the populations in Appendix 3 I have thought it undesirable to attempt extrapolation. I am aware that some of the temperature means arrived at are open to criticism ; but all have been calculated as objectively as possible and the correlations that are about to be described show that in general the methods employed are valid.

WING-LENGTH IN RELATION TO ALTITUDE (AIR-PRESSURE) AND TEMPERATURE

In Text-figs. 1-3 the mean wing-lengths detailed in Appendix 3 are plotted respectively against altitude, minimum temperature and maximum temperature (as defined previously). In some respects these diagrams are illuminating, but they can, as will be shown, also be thoroughly misleading, for the reason that the three environmental factors are not independent.

In order to separate the effects of altitude and temperature, partial regression coefficients have been calculated, which give a measure of the influence that each

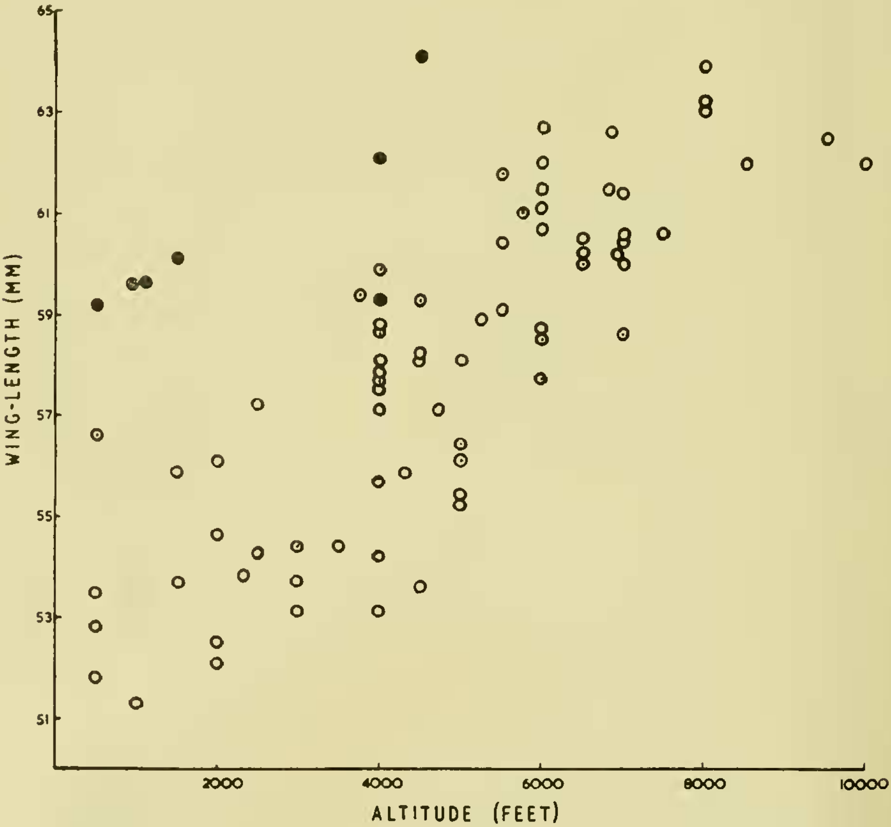


FIG. 1. Wing-length/altitude correlations. (Black circles, South African populations; dotted circles southern tropical.)

factor would have if it varied while the others remained constant. If w = wing-length (in mm.), a = altitude (in thousands of feet), n = minimum temperature (°F.) and x = maximum (°F.) the partial regression equation is :

$$w = 59{\cdot}8 + 0{\cdot}69a - 0{\cdot}28n + 0{\cdot}12x.$$

Each of these regression coefficients is highly significant statistically, since their standard errors are only 0·13, 0·04 and 0·05 respectively. It is to be noted, however, that each cofficient represents an average, and the data do not suffice for an investigation of whether the relationship in each case is rectilinear or not. From the purely statistical point of view the equation fits the observed data so closely as to warrant the conclusion that no environmental factor having a comparable

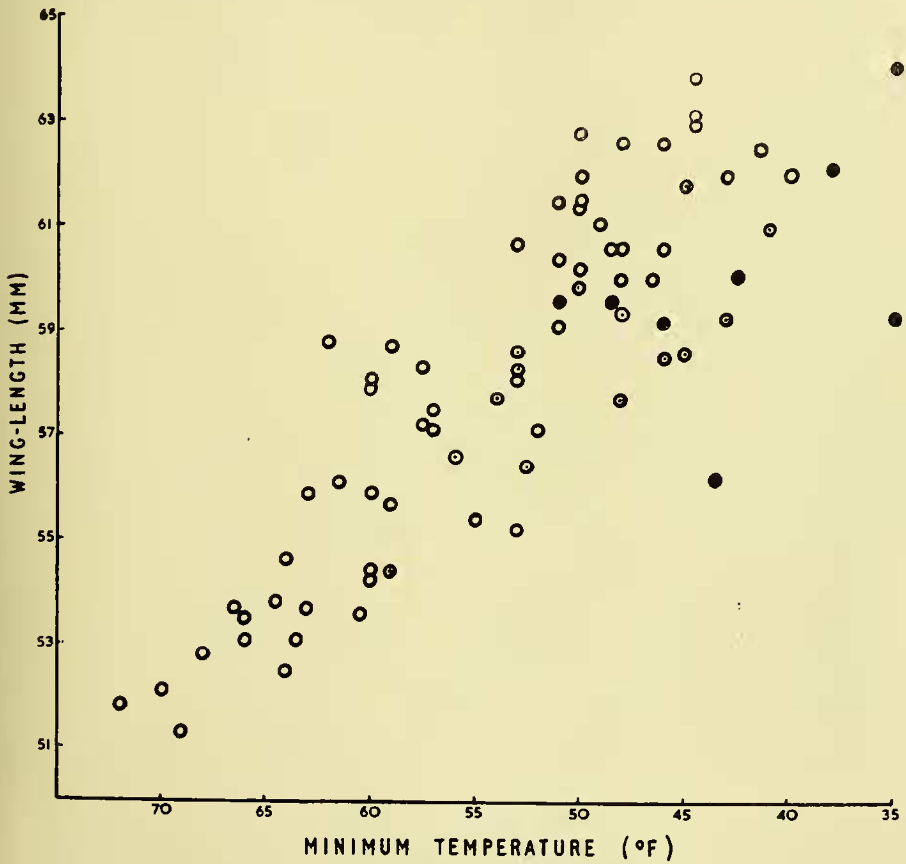


FIG. 2. Wing-length/minima correlations.

effect on the wing-length remains unconsidered. From the biological point of view this is in at least one respect questionable, as will appear.

Meanwhile, subject to these comments, it is concluded from the equation that on the average, over Africa as a whole :

(1) *Zosterops* wings tend to increase 0·69 mm. for every 1,000 ft. of altitude. Since the altitude range of the combined *Zosterops* habitats is 10,000 ft., the total potential effect of this factor is about 7 mm. (12% of the overall mean wing-length).

(2) *Zosterops* wings tend to decrease 2·8 mm. for each rise of 10° F. in the minimum. With extremes of mean minima 35° and 72° F. (Appendix 3), the total potential effect is about 10 mm. (17% of the overall mean wing-length).

(3) *Zosterops* wings tend to increase in length by 1·2 mm. for each 10° F.

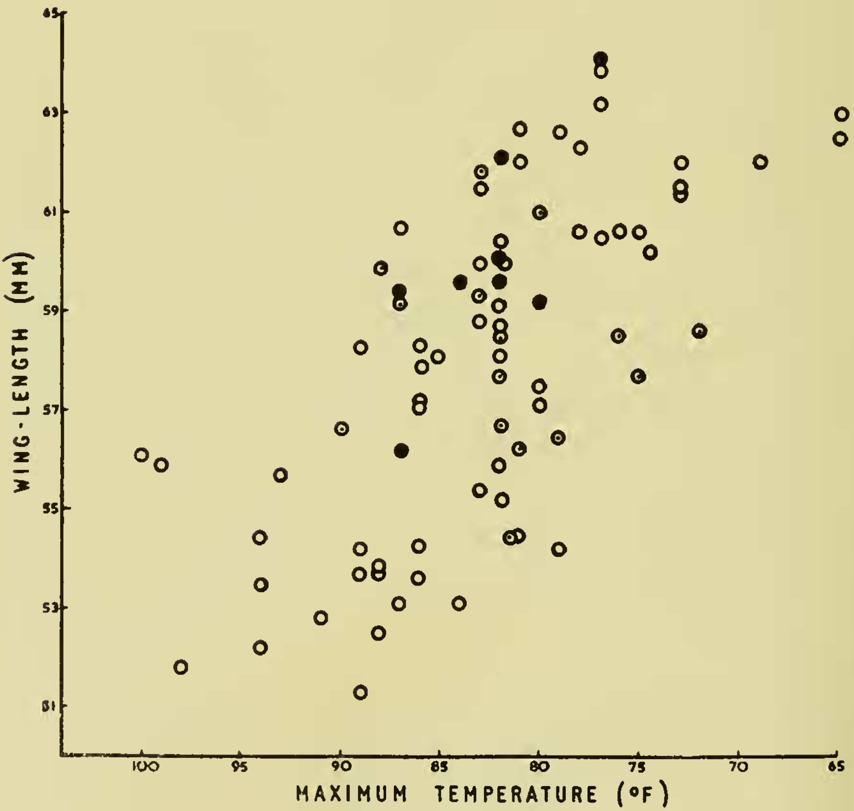


FIG. 3. Wing-length/maxima correlations.

rise in maximum temperature of the environment. Since the lowest maximum in Appendix 3 is 65° F. and the highest 100°, the total potential difference in wing-length attributable to this cause in Africa is only about 4 mm. (7% of the overall mean wing-length).

Wing-length and altitude

The equation shows that altitude has an important effect on wing-length that has nothing to do with temperature and hence presumably operates through the reduced air-pressure. No conclusive evidence of such an effect appears to have been presented hitherto for any type of bird. Long critical series of weights and wing-areas would be required for a closer examination of this phenomenon.

Since changes in air-pressure purport to be a direct cause of the changes in wing-length, then, when changes of pressure with altitude are plotted along with the changes in the " lift " provided by the wing, i.e w^2, the two " curves " might be expected to be of similar form. In fact they are not, because the pressure/altitude curve is very close to a straight line, while that of altitude/w^2 is quite different. The explanation may be complex. There is the purely statistical point that the addition of 0·69 mm. to the wing-length per 1,000 feet, is an average one ; as already noted, this may conceal a non-rectilinear relationship that the data are not " good " enough to disclose. Another, and strong, possibility is that the relationship between the wing-length and the mass of the bird is disturbed by various anatomical adjustments necessitated by changes in air-pressure. For example, in the species investigated by Norris and Williamson (1955) the ratio of heart-weight to total weight increased with the altitude at which the birds lived ; and similar changes in lung-capacity may be expected.

Text-fig. 1 shows that no population of small *Zosterops*, with wing averaging less than 58 mm., occurs above 5,000 ft. Another prominent feature of Fig. 1 is the grouping of the South African populations (black circles). Their appearance of being long-winged for their altitudes is undoubtedly due to the fact that South African temperatures are lower than those of tropical Africa at the same altitudes (cf. Appendix 3) ; it will be seen that this segregation of the South African points is not repeated when the wing-lengths are plotted against the minimum temperatures (Text-fig. 2).

It may also be noted in Text-fig. 1 that the populations of the highest altitudes, those of the upper levels of Mt. Kenya and of the Kivu volcanos, appear to consist of birds a little smaller than might have been expected. If this is genuine it might be a result of the following factors: (*a*) gene-flow, of necessity predominantly from lower altitudes, where the birds are smaller ; (*b*) marginal ecological conditions, implying poorer feeding—the hypothesis put forward by Davis (1938) to account for the unexpectedly small size of some mountain populations of rodents.

Wing-length and minimum temperature

The partial regression equation given above shows that wing-length increases as minimum temperature decreases—which is in accord with Bergmann's rule—and that this factor operates more powerfully than the others under consideration. Moreover, as shown by the consistent grouping of the points in Text-fig. 2 along an approximately straight line, this temperature factor (in conjunction with altitude) overrides any ecological adaptation, even though the populations involved occupy habitats as different as evergreen forest and dry thorn-bush. The consistency of the combined effect is further illustrated by the following facts extracted from Appendix 3 :

(1) Where populations otherwise similar are subjected to different minimum temperatures (and altitudes), those birds inhabiting the cooler climate have longer wings in 18 out of the 19 groups of comparable populations. (In these cases of course the altitude and minimum-temperature factors are reinforcing each other.) The only exception occurs in populations 59–64, and there the difference on the "wrong" side is extremely small.

(2) The five savanna populations on the south of the Sahara, nos. 14–18, range in wing-average only from 53·5 to 56·1 and the minima from 62° to 67° F. Yet even within these narrow limits the correlation is so effective that the populations with the shortest wings, 53·5 and 53·7, occur with the highest minimum temperatures, 66° and 67° F., and the other three wing-lengths are in inverse order of the temperatures.

(3) On the eastern rim of the Congo Basin, as already noted, on a line some 70 miles long from Kamituga eastwards (populations 52–54) mean wing-lengths fall from 61·4 mm. with minimum 50° (at 7,000 ft.) through 55·9 with 60° F. (at 4,300 ft.) to 53·1 mm. with 66° F. (at 3,000 ft.)—another case in which altitude and temperature are operating together.

The only local peculiarity disclosed by Text-fig. 2 is that the South African populations (black circles), grouped as they are to the right, have rather shorter wings than would be expected from the low minimum temperatures. Since among the African Zosteropidae they alone are outside the tropics, the first suspicion is that we have here a " latitude effect " such as Snow (1953) demonstrated in the Paridae. He suggested that in the short daylight of winter the high-latitude tits could not maintain a body of the size most efficient for heat-conservation. This could hardly apply to South African birds, the duration of whose feeding days in winter would be only 2–3 hours shorter than those on the equator—and much longer than those in the latitude of Britain ; but I can think of no acceptable ecological reason why South African *Zosterops* should show this peculiarity.

Among the South African birds two populations are outstanding, namely the *pallida* of the south-west and the (higher-altitude) *pallida* of the Orange Free State. Both have conspicuously shorter wings than might have been expected from the low minimum temperatures—which are well based on local meteorological records. This effect is the more remarkable because the maximum temperatures are rather high and hence favour lengthening of the wing.

In connection with this peculiarity of *pallida* two possibilities may be suggested. First, the bodies may be stunted as an adaptation to rigorous ecological conditions.

This seems unlikely because, although the environment of South West Africa, with its aridity and extreme daily range in temperature, is one of the harshest experienced by *Zosterops*, in the Orange Free State, especially along the Vaal River, whence some of the specimens come, conditions are not so bad. The alternative possibility is that in this *Zosterops* the wing is abnormally small for the body. No data exist for testing this: but these birds show another peculiarity that is presumably not independent, namely an extremely high ratio of tail-length to wing-length, as is obvious in Text-fig. 5.

Wing-length and maximum temperature

The statistical demonstration that the wings of African *Zosterops* tend to get longer as the maximum temperature rises is contrary to Bergmann's rule. It is also contrary to the impression given by Text-fig. 3, but this is undoubtedly fallacious and due to the fact that (as shown by the equation) minimum temperatures and altitude have, in combination, an effect on wing-length powerful enough completely to mask the influence of the maximum temperature. Here, then, in Text-fig. 3 we have an outstanding example of the misleading result that can be produced by the use of a graphical method unchecked by statistical analysis.

The tendency for wing-length to increase with a rise in the maximum temperature is difficult to explain on biological grounds, because the reverse would be expected. It should, however, first be pointed out that temperature is not an adequate index of the demands made by the environment on the bird's potentiality for heat exchange, because evaporation depends greatly also on the relative humidity of the air. This is subject to wide local variation according to the general climate and cannot be neglected when the effects of maximum temperatures on heat-exchange are being considered.[1] Far too few stations record relative humidities for it to be possible to calculate the mean saturation-deficits experienced in the hot season by any of the populations under discussion. All that can be said, from a knowledge of the climatic régimes, is that more of the very high maxima are accompanied by low humidities, and hence are biologically less exacting, than are accompanied by high humidities. And it is virtually certain that if the populations could be arranged in order of the saturation-deficits they experience in the hot season it would differ a good deal from that of their hot-season maximum temperatures.

In birds exposed to the greatest heat some special adaptations for escaping or reducing the full effect may be present—faster breathing with or without gaping, a higher ratio of surface (internal and/or external) to mass, thinner plumage, or a persistent seeking of the coolest available eco-climates.

Wing-length and other temperature combinations

It has been suggested that it might be interesting to ascertain whether statistically significant correlations exist between wing-length, annual mean temperature (*m*)

[1] This does not apply to minimum temperatures, which are practically always accompanied by high humidities, if not by dew-fall.

and annual range in temperature (r), m being $\frac{\text{max.} + \text{min.}}{2}$ and r max. — min. The partial regression equation with altitude then becomes:

$$w = 59{\cdot}8 + 0{\cdot}69a + 0{\cdot}20r - 0{\cdot}16m.$$

(Standard errors of both m and r are ·04, so that both coefficients are highly significant.) This means that wings tend to be shorter with higher means and to be longer with greater annual ranges. The effect of the higher mean would be in conformity with Bergmann's rule; and the effect of the higher annual range is what would have been expected from the first equation. For annual range is a reflection of both higher maxima and lower minima; and each of these factors was shown to be correlated with longer wings.

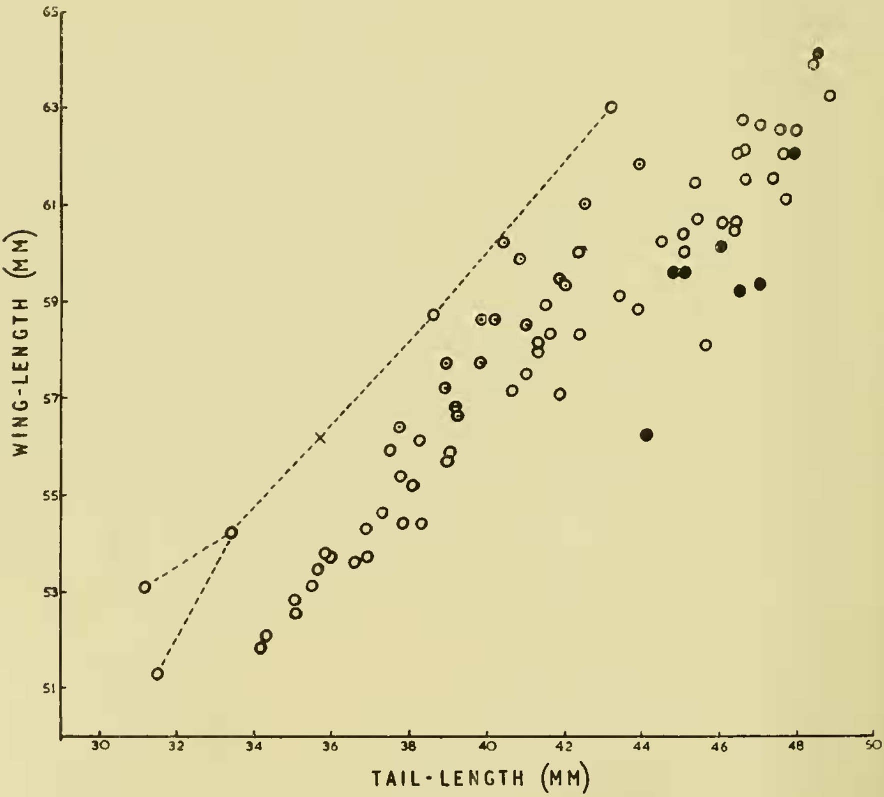


FIG. 4. Wing-length/tail-length correlations.

TAIL-LENGTH IN RELATION TO WING-LENGTH AND ENVIRONMENT

Mean tail-lengths vary from 31·2 to 48·7 mm. and the correlation between mean tail-length and mean wing-length is remarkably high, + 0·93—cf. the grouping in Text-fig. 4. Conformably, the equation showing the multiple regression of tail-length (t) on altitude, minimum temperature and maximum temperature takes exactly the same form as that of wing-length (p. 329), being :

$$t = 44{\cdot}0 + 0{\cdot}73a - 0{\cdot}44n + 0{\cdot}21x.$$

Again, these figures are highly significant statistically (standard errors 0·19, 0·05 and 0·07 respectively) and they mean that the tails tend to increase with altitude, with fall in minima and with rise in maxima. These effects can, however, be shown to be due almost entirely to the closeness of the correlations between wing-length

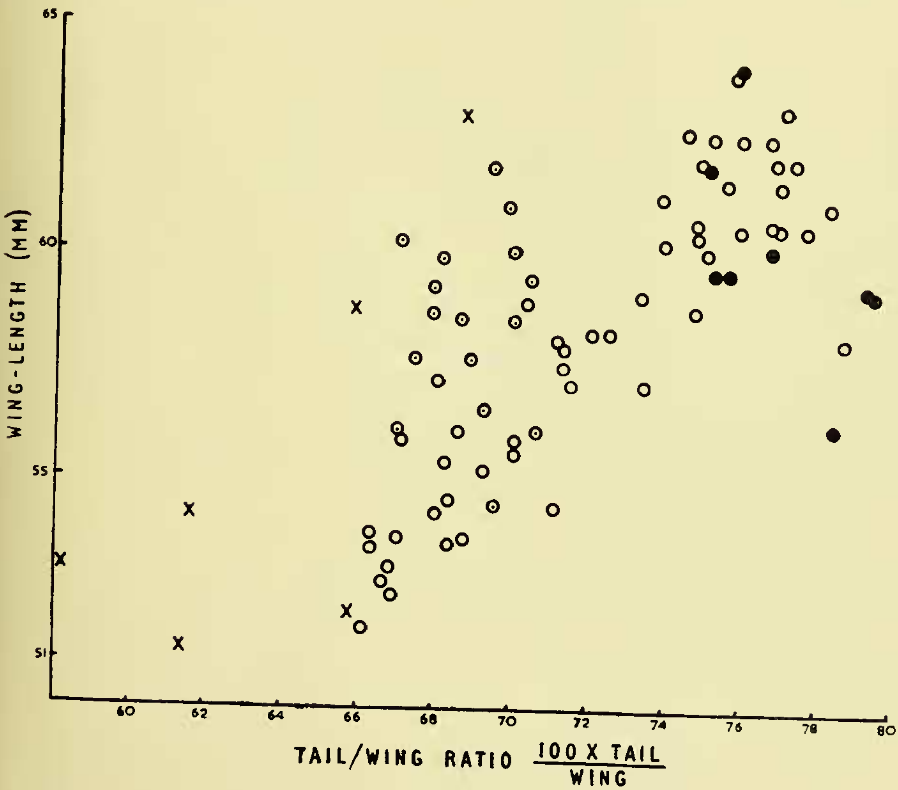


FIG. 5. Correlations between wing-length and tail/wing ratio.

and tail-length because, when the multiple regression of tail-length is calculated on wing-length together with the other factors, the equation becomes :

$$t = -30{\cdot}50 - 0{\cdot}120a - {\cdot}92n + 0{\cdot}062x + 1{\cdot}246w.$$

Of these the wing factor (w) is highly significant (standard error 0·114), the minimum temperature is just significant (standard error 0·45) and the others are not significant.

Reverting to the first of these two equations, and applying the same method as was used with the wings (p. 330), it can be inferred that in the African *Zosterops* the potential total effect of altitude on tail-length is 7 mm., of minimum temperature 15 mm., and of maximum temperature 7 mm. These figures, 17%, 37% and 17% respectively of the overall mean tail-length, are proportionately greater than the corresponding effects, 12%, 17% and 7%, of the respective factors on the wing. Hence, compared with the wing, the tail is relatively more sensitive to the effect of temperature than to that of altitude. This is confirmed by the last equation, in which it is shown that minimum temperature has a significant influence (along with wing-length) on tail-length, but that altitude has not. This result accords with the probability that variations in air-pressure may not exercize a strong and direct influence on tail-length ; and certainly not so strong as on wing-length.

As shown in Text-fig. 5, the tail/wing ratio rises with increasing wing-length ; in fact, even omitting the abnormal Cameroons group (marked × in Text-fig. 5), in the shortest-winged populations the tails average only about 67% of the length of the wings, while in the longest-winged tails average about 76%.[1] It is shown by the last equation that this is unlikely to be due to a direct altitude effect, i.e. to depend on air-pressure (cf. the scatter when tail/wing ratios are plotted against altitude in Text-fig. 6), but the possibility of a temperature effect is not excluded. Thus, the African *Zosterops* seem to show the same phenomenon as the Palaearctic Paridae, in which tails are proportionately longer in colder climates (Snow, 1953). It is possible that the same holds good in Malaysian birds generally (Longhurst, 1952), but the climatic data cited for these leave something to be desired. This result is terminologically at variance with Allen's rule, under which extremities are proportionately shorter in cooler climates ; but this rule is probably not applicable to an appendage such as a bird's tail, in which there is no circulation and the heat-exchange is presumably negligible.

The biological reason for the progressive change in the tail/wing ratio of the African *Zosterops* is difficult to suggest. I owe to Mr. Bernard Stonehouse the idea that if, as appears, the *Zosterops* inhabiting the cooler climates have more ample contour feathers, then the other feathers might share in the process of elongation ; and owing to the less specialized nature and function of the tail-feathers this process might in them be less subject to modification by natural selection than in the flight-feathers.

There are no marked discontinuities in Text-fig. 4 although two geographical

[1] Since the above was written I have received Mees' paper in *Sarawak Mus. J.*, **6** (1955) : 641–661, in which he describes a similar change in tail/wing ratio with wing-length in certain eastern Zosteropidae.

groups occupy slightly aberrant positions. Moreover, in these two groups the alignment of the points is parallel to that of the main body. It can be concluded that the same principles are operating in all forms of *Zosterops* and that there is no over-riding adaptation of tail/wing ratio to habitat (in particular, to open thorn-bush as against evergreen forest).

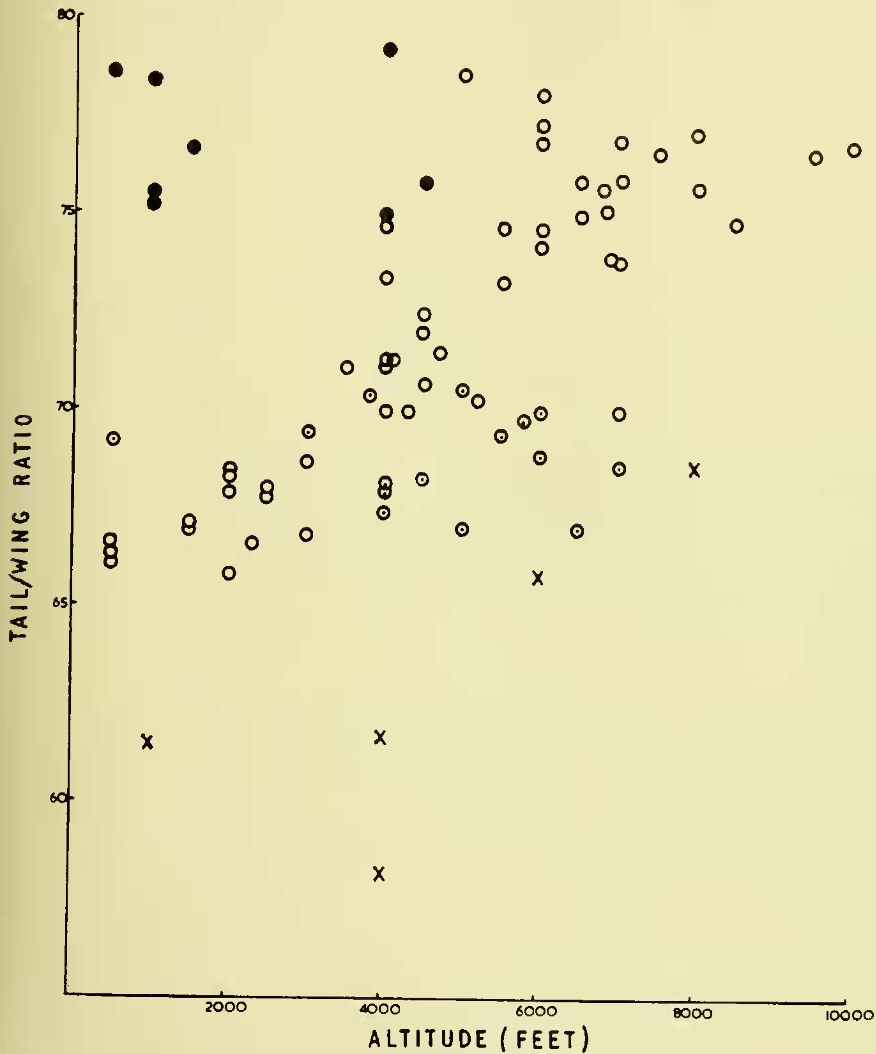


FIG. 6. Correlations between tail/wing ratio and altitude.

In Text-fig. 4 certain populations, 19–23 and 66 in Appendix 3, lie to the left (open circles joined by the broken line), that is, their tails are abnormally short in relation to their wings. The segregation of 19–23 is equally marked in Text-figs. 6 and 7, where tail/wing ratio is plotted against altitude and minima respectively. All the populations concerned lie round the head of the Gulf of Guinea on and near Cameroon Mt. (see Map 5), except 66, which is in Tanganyika. Moreover the tail/wing ratio of the birds of Fernando Po (× in Text-fig. 4), which are identical in plumage, lie on the same line exactly. The biggest bird in this series (wing 63 mm.), from the

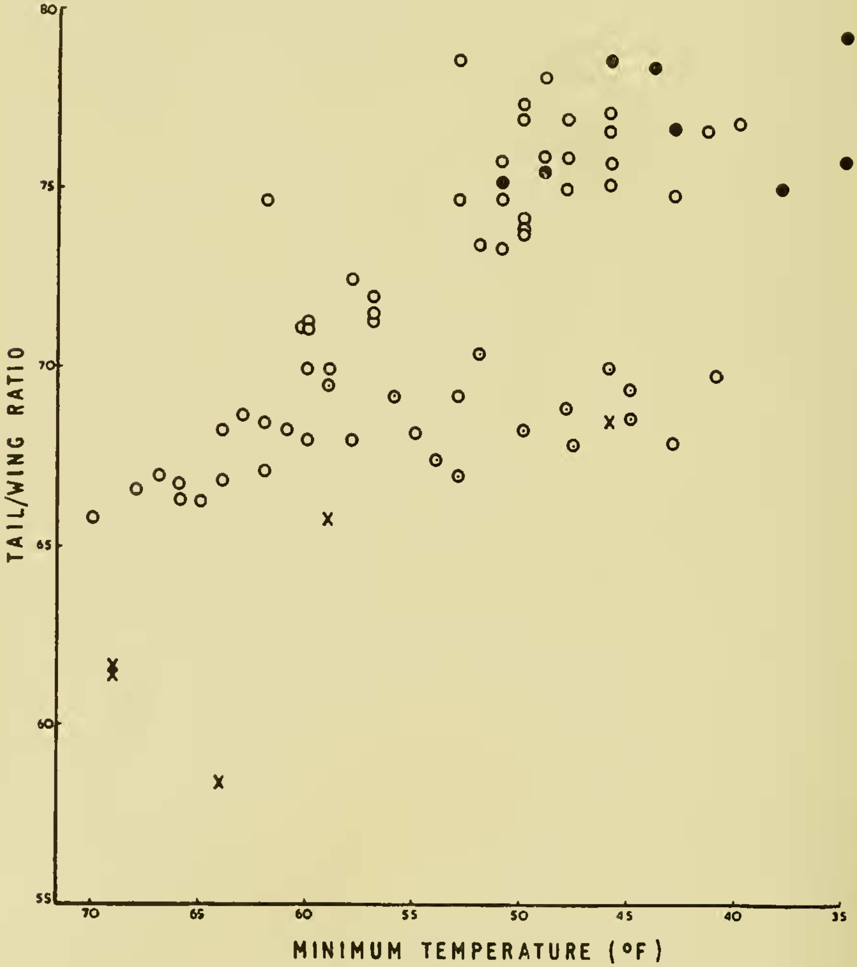


FIG. 7. Correlations between tail/wing ratio and minima.

top of Cameroon Mt., is so generally aberrant as to be placed in a different genus (*Speirops*), but nevertheless its tail/wing ratio is on the same, abnormal, line as those of its unrelated neighbours. This suggests that the character " short tail " in the other Gulf of Guinea birds may not be of taxonomic significance, but is related to some ecological peculiarity of the area.

The South African populations (usually attributed to at least two different species) are not completely separated in Text-fig. 4 (black circles) from the remainder, as are those of the Cameroons, but they do all lie to the right, having their tails abnormally long for their wings. It seems unlikely that this can be correlated with some peculiar environmental factor, because the birds concerned inhabit an extremely wide range of habitats (as described in Part 4).

BEAK-LENGTH IN RELATION TO WING-LENGTH AND ENVIRONMENT

Correlation between beak-length and wing-length is high, + 0·83. The partial regression equation for beak-length (b) on altitude, minimum and maximum temperatures is of the same pattern as those for wing and for tail, namely :

$$b = 14{\cdot}11 \text{ mm.} + 0{\cdot}144a - 0{\cdot}039n + 0{\cdot}005x.$$

In this equation a and n are significant, with standard errors 0·04 and 0·012 respectively, but x is not. Hence it is inferred that altitude and minimum temperature each affect beak-length, in the same way as they do wing-length, but to the same potential extent, each up to a total of 1·5 mm.

If now, as in the case of tails, the partial regression of beak-length is calculated on wing-length as well as on the environmental factors, the equation is :

$$b = + 0{\cdot}44 - 0{\cdot}013a + 0{\cdot}25n - 0{\cdot}022x + 0{\cdot}229w.$$

Again, the last factor, wing-length, is highly significant (standard error ·031), the minimum temperature just significant (standard error ·012) and the altitude and maximum temperature not significant. This means that the over-riding factor in determining the length of the beak is the length of the wing (i.e. presumably the general size of the bird), but that there is also a slight tendency for beak-length to increase with higher night temperatures. This would accord with Allen's rule, under which exposed, terminal, parts of the body are proportionately longer in warmer climates.

When beak-length is plotted against wing-length (Text-fig. 8), the data look homogeneous. Points relating to birds of dry country are not segregated from those of forest. Hence there is no important adaptation of beak-length to type of habitat or type of tree.

In Text-fig. 8 it will be seen that as a whole the southern tropical populations (distinguished by a dot in the circle), some of which live in savanna and some in mountain forest, have a beak-length that is nearly constant in spite of differences in wing-length. This is interesting because the populations comprising this southern group have usually been divided between two species.

With one exception, the *Speirops* of the top of Cameroon Mt., the beaks that are longest in relation to wings all belong to birds of the highlands of Abyssinia, eastern Kenya and north-eastern Tanganyika (squares on Text-fig. 8), a group of populations there are other grounds for thinking closely allied. In this respect (though the differences are very small) they stand apart from the *Zosterops* of the other high mountains of Central Africa and western Kenya. For this no ecological reason can be suggested, since all the mountains are characterized by evergreen forest and this is represented by the same type, though not exclusively, in both areas.

The two populations with proportionately the longest beaks of all are those (otherwise different in both dimensions and plumage) confined to the tops of the

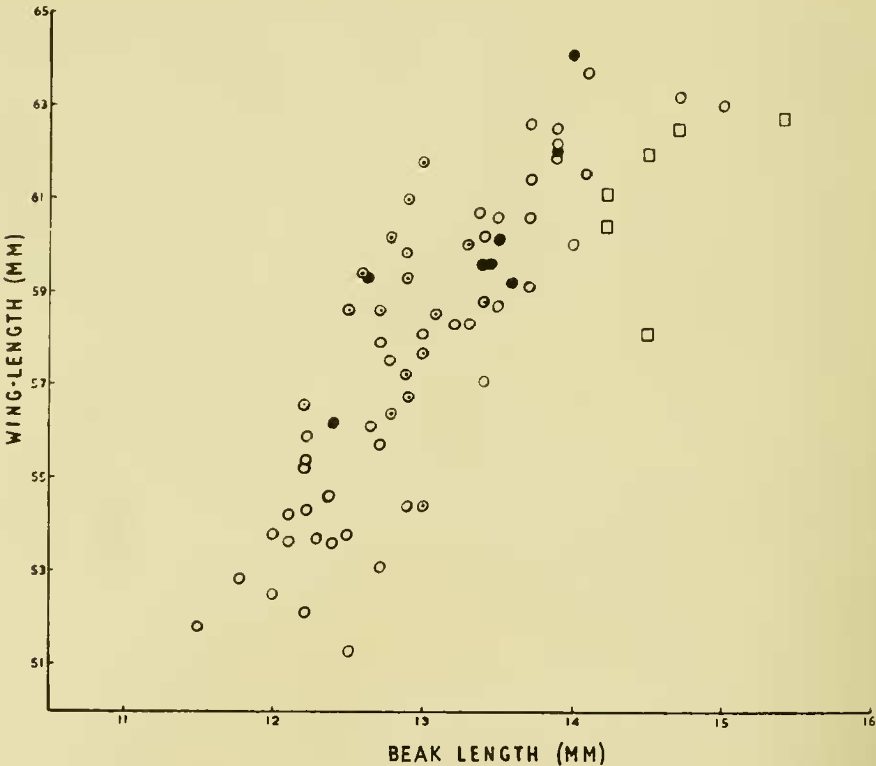


FIG. 8. Wing-length/beak correlations.

widely separated Kulal and Teita Mountains (populations 28 and 34 in Appendix 3). Again, no ecological reason can be suggested. The number of individuals on each mountain is certainly small, so that in this respect conditions are from the evolutionary point of view more comparable with that of a bird-population on an oceanic islet than of one living in a continent.

DIMENSIONAL CORRELATIONS AND TAXONOMY

The one bird of undoubted taxonomic distinctness at a high level, the *Speirops*, is abnormal in only one of these correlations, namely tail/wing ratio, and in that it agrees with its immediate neighbours.

On the other hand, there are four groups that show some peculiarity not explained on ecological grounds, which might therefore be regarded as primarily phylogenetic:—

South African birds (black circles in text-figs.). On the whole these are unusually long-winged (? large) for their altitudes and somewhat short-winged (? small) for their cold-season minima, especially in the case of *pallida*. They also tend to have high tail/wing ratios and they are segregated from other African *Zosterops* when this ratio is plotted against altitude (Text-fig. 6) and, less sharply, against minimum temperature (Text-fig. 7). In this respect also, *pallida* is the most divergent of the South African birds.

Southern tropical populations (dotted circles in text-figs.). These birds are geographically contiguous with the South African, but they differ markedly from them in their tail/wing ratios: the points in Text-fig. 5 are distributed in two parallel linear groups. This segregation is noticeable also when tail/wing ratios are plotted against altitude (Text-fig. 6) and against minima (Text-fig. 7). Also the southern tropical birds tend to have beaks of much the same length while their wing-length varies. These facts suggest that the southern tropical birds form a single species distinct from the South African birds.

Cameroons group (crosses in text-figs.). The tail/wing ratio is aberrant (Text-fig. 5) not only in itself but also in relation to altitude (Text-fig. 6) and minima (Text-fig. 7). But because this peculiarity is shared by the local *Speirops* it is thought not to be of taxonomic significance.

East and northeast African montane birds. The beak/wing ratio of these birds, commonly divided into several species, is consistently high.

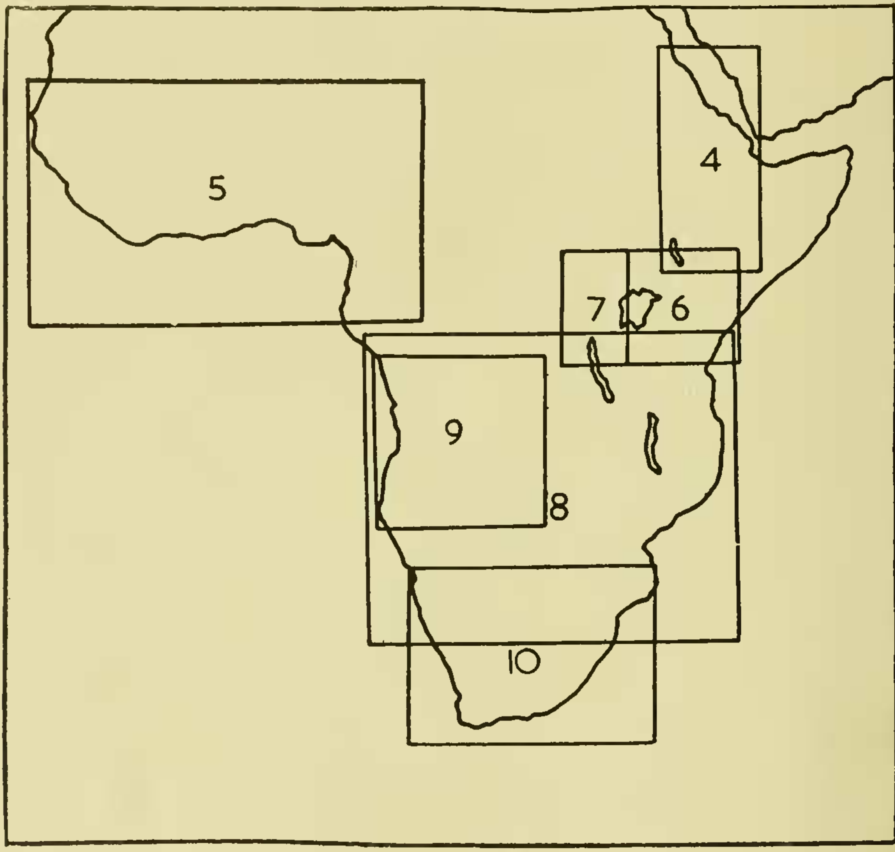
Conclusion. The foregoing analyses disclose correlations of dimensions with each other and with environmental factors that are remarkable for their general application throughout the continental African Zosteropidae. There are no abnormalities so striking as to provide compelling reasons for separating populations at the specific level, though peculiarities exist that may serve as ancillary characters, to be considered in cases of disputed relationships.

The dimensions of insular populations, which are given in supplementary tables in Appendix 3, do not lend themselves to statistical analysis on the same lines as the continental data. The results obtained above give, however, standards of comparison, utilized in Part 5.

PART 4

CONTINENTAL POPULATIONS: CHARACTERS AND INTERGRADATIONS

In this part the *Zosterops* of Africa will be described in six geographical sections (see Map 3 for key to local maps), an arrangement adopted in order to assist



MAP 3. Key to area maps.

exposition of the complicated material. At the end of each section the main outlines will be summarized and the appropriate nomenclature indicated. The taxonomic arrangement at the specific level is discussed as a whole in the general synthesis (Part 6); meanwhile, the results have been anticipated in Part 1 and sketched in Map 1. Throughout the sections that follow, the discussion will be in the light of the correlations and general principles dealt with in Parts 2 and 3.

NORTH-EAST AFRICA

Throughout Eritrea, Abyssinia and Somaliland the lowlands are dry, with acacias and combretums as the dominant trees ; and the east and southeast are particularly arid. The highlands still carry patches of evergreen forest, largely in its driest form (dominated by *Juniperus procera*), but richer in the more humid south-west of Abyssinia.

The *Zosterops* situation is most complicated and interpretation is hindered by the lack of field data. Six main forms exist, the habitats and chief characters of which are outlined in Table I. The last two (highland) forms have always been regarded as specifically distinct, both from each other and from the lowland forms. The latter conclusion is no doubt correct, the former probably not (see below).

TABLE I.—*Main Characters and Habitats of the* Zosterops *of N.E. Africa.*

Range.	Habitat.	Name used by Sclater (1930).	Colour of Upper parts.	Colour of Belly.
N. and E., lower altitudes (up to 5,000 ft.)	Any arborescent vegetation (Erlanger 1907, K. D. Smith *in litt.*)	*abyssinica*	Grey-green	Greyish
S. E., lower altitudes (up to 6,000 ft.)	Dry acacia country (Erlanger 1907). Thorn scrub and, exceptionally, juniper woods (Benson 1946*b*)	*smithi*	Greyish yellow-green	Yellow
N.W., lower altitudes (up to 6,000 ft.)	" Steppe " (Neumann 1906)	*senegalensis*	Yellow-green	Yellow
S.E., lower altitudes (up to 6,000 ft.)	" River valleys " (*ibid.*) Deciduous forest (Cheesman *in litt.*)	*omoensis*	Yellow-green	Greyish
Western highlands (4,500–9,000 ft.)	Mountain forest (Neumann 1906)	*kaffensis*	Rich green	Yellow
Highlands elsewhere (5,000–10,500 ft.)	Evergreen forest (cf. Benson 1946*b*)	*poliogastra*	Rich green	Grey

The geographical distribution of the six forms is shown diagrammatically in Text-fig. 9. It will be seen that a grey-bellied and a yellow-bellied form divide the highlands between them, while round them at lower altitudes are arranged four other forms, alternately grey-, yellow-, grey- and yellow-bellied. Of the four lowland birds the two occupying western Abyssinia, which is damper than the east, are more richly pigmented than the others.

The actual records of the various forms are plotted in Map 4, which gives some indication of the complicated relief. Clearly the concept of sympatry and allopatry is not easy to apply. Lowland forms penetrate deeply into the highlands: along the Rift Valley a line of lowland grey-belly localities separates the eastern from the western highland grey-belly populations, while in the south-west the other lowland

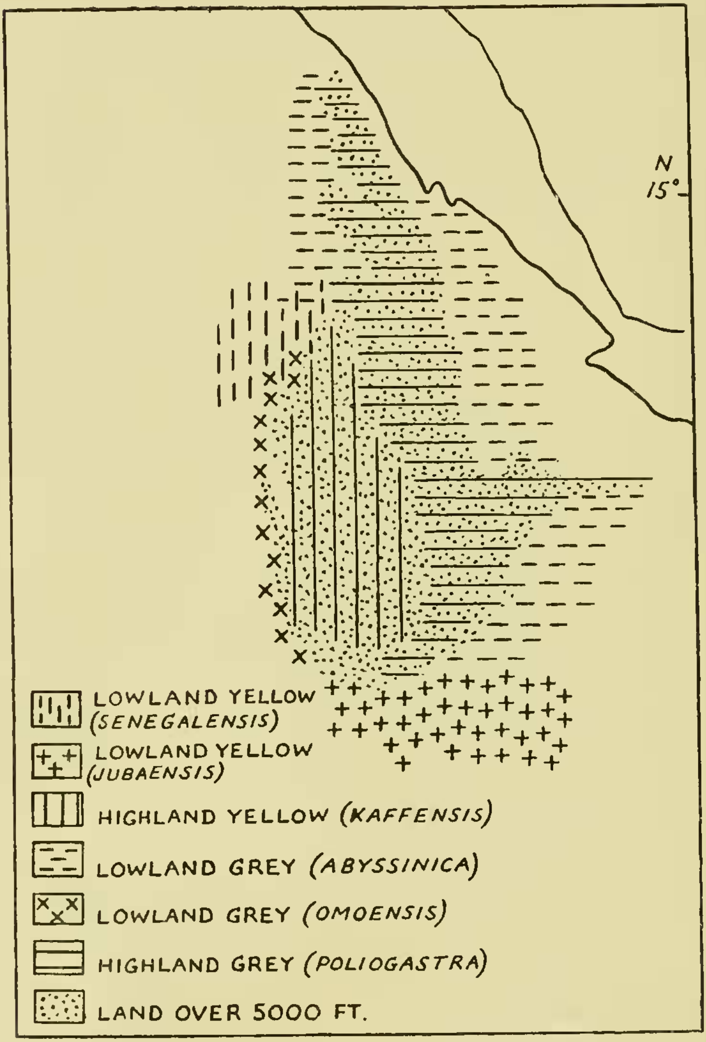
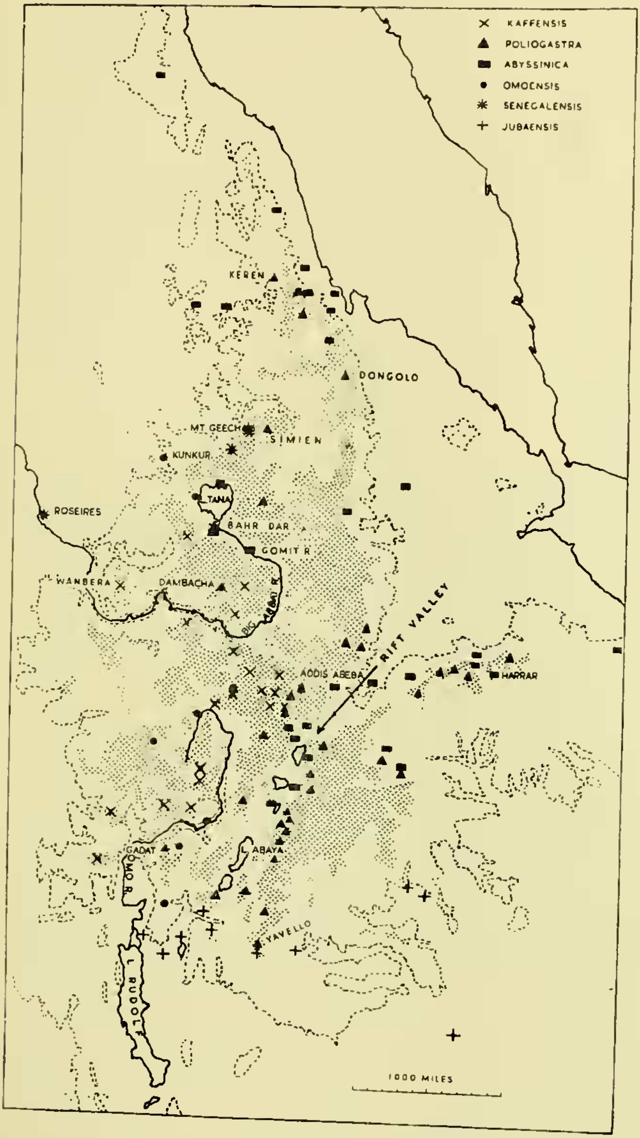


FIG. 9. Distribution (diagrammatic) of *Zosterops* belly-colour in N.E. Africa.



MAP 4. *Zosterops* distribution in N.E. Africa.

grey-belly (*omoensis*) occupies the Omo River valley, deeply cut through the country of the highland yellow-belly (*kaffensis*). Highland and lowland forms must in places actually meet. Two lowlands forms and also *poliogastra* have been recorded from Keren (Reichenow, 1903; Zedlitz, 1911), but this is an area of extremely broken country and it may be doubted whether the locality is critically stated. However, the specimens (in the British Museum) of both (grey-bellied) lowland *omoensis* and (yellow-bellied) highland *kaffensis* from Roke suggest overlap there; and there is a specimen of *abyssinica* from 9,000 ft. (= 2,750 m.), as noted on the label, at Bijo, near Harrar, right in the highland (*poliogastra*) zone. Again, Benson (1946*b*) at the extreme south of the range of *poliogastra*, near Alghe, recorded both this and the local lowland birds in juniper woods at 6,000 ft. (= 1,800 m.). One specimen from near Keren may be a hybrid between the highland *poliogastra* and the lowland *abyssinica* (see Note 4, Appendix 1). Finally, Mr. K. D. Smith (*in litt.*) encountered a mixed party of *abyssinica* and *poliogastra* at Faghena, on the eastern escarpment of Eritrea, on exotic trees in a clearing in the woodlands at 5,570 ft. This is an abnormally low altitude for *poliogastra* and the whole locality is peculiar ecologically.

The highland birds

In the highlands the grey-bellies (*poliogastra*) have a more extensive range than the yellow-bellies (*kaffensis*; see Note 5, Appendix 1). They occur all down the spine of the Eritrean and Abyssinian highlands, west over the plateau to near Lake Tana, east along the mountains towards Harrar and south to the end of the high country, at Yavello, east of the tip of Lake Rudolf. Grey-bellies everywhere occur on both sides of the line of the Abyssinian lakes, but they do not cross the deeply-cut valley of the Omo River just to the west. Beyond this the high-level *Zosterops* are yellow-bellies, which range from Lake Tana southwards.

The two forms apparently overlap a little. Both occur at Addis Ababa, with the yellows much the commoner (Guichard, 1950, and *in litt.*), and in the neighbouring Menengasha forest (B.M. specimens). The Addis overlap may be a recent recolonization following tree-planting of the formerly deforested area. Away to the north-west, south of Lake Tana, the Dembacha grey-belly (B.M. specimen; breeding condition), which is partly surrounded by yellow-belly localities, may indicate another limited area of overlap.

Both the grey-bellies and the yellow-bellies show some geographical variation. The former are a trifle smaller in the extreme southwest of their range (mean wing 61·5 mm. compared with 63·9). For an alleged plumage-difference between northern and southern grey-bellies, see Note 6, Appendix 1. Of the highland yellow-bellies (see Note 5, Appendix 1), those south of Nono are the most richly coloured, both above and below, and those from Shoa (the neighbourhood of Addis Ababa) which have been distinguished subspecifically, are the biggest, and a little duller generally, without such large and bright yellow foreheads. But, again, those from Nono and further north, within the bend of the Big Abbai (Blue Nile) are intermediate in these characters. Thus the variation is not a simple geographical cline and moreover plumage-colour is not correlated with rainfall.

I believe that the grey-bellies and the yellow-bellies of the highlands are conspecific. In the middle of their range both forms are the same size, with the same tail/wing ratio, and are similar in plumage (including eye-ring), except for the belly. Pending further field data, it seems that they form a parallel to the cases of the grey-bellies and green-bellies in the Cape (see section on " South Africa " below). True, in Abyssinia there is no evidence of interbreeding, but the ornithology of the country is such that it could hardly be expected at the present stage.

With their sharply defined yellow foreheads and comparatively long tails (ratio 75) the yellow-bellies of the western Abyssinian highlands differ from the nearest montane birds, on the Imatong group on the Sudan border, which have dimmer foreheads and shorter tails (70). The Abyssinian birds are more like some Kenya highlands birds, and though they differ from the nearest of these in having stronger carotenoid these appear taxonomically closer than the Imatong birds.

The lowland birds

As already mentioned, there are four main forms arranged round the highlands, grey-bellies and yellow-bellies alternately. In these birds also belly-colour has always been taken as a specific character but, as shown in Part 2, there is no reason to think this is correct and their true relationships are difficult to decide. All four forms are, as expected, smaller than the highland birds (see Appendix 3). The two eastern ones are particularly dingy in plumage, with reduced carotenoid and a tendency to muddy brownish wash on the underparts. These characters are not shared by the two western birds, the yellow-bellied *senegalensis*, which reaches Lake Tana from West Africa, and the lowland bird of south-west Abyssinia, with its clear grey belly (*omoensis*).

The difference in general colour tone between the eastern pair and the western pair of birds is connected with the fact that, apart from stronger carotenoid in the west, the melanin in these birds is of black (A) type, while in the eastern pair of birds it is of the browner (B) type. As discussed in Part 2, the taxonomic value of this character is uncertain. In so far as it depends on the humidity or aridity of the environment, as in South Africa, it is worthless. But in the West African *senegalensis* it has been shown that the melanin is of (A) type even in the driest environment. The occurrence of the same character in the contiguous *omoensis* might therefore mean taxonomic affinity ; but since *omoensis* inhabits the wettest environment of all the lowland birds, it might alternatively be, as hitherto believed, a form of *abyssinica*, climatically modified.

Geographical relations between lowland forms

The grey-bellies of the eastern lowlands extend from the Red Sea Hills (Erkowit) of the Sudan " wherever there is thick vegetation " (Cave and Macdonald, 1955) all down the eastern foot of the Eritrean–Abyssinian plateau ; and thence through the Rift Valley nearly to Lake Abaya and east through British Somaliland. They also occur down the western side of the Eritrean and Abyssinian highlands as far as Lake Tana and the beginning of the Blue Nile (Great Abbai) valley. Here they seem to overlap the yellow-bellies (*senegalensis*) from the west, which find their eastern limits on the western slopes of these Eritrean and Abyssinian highlands. Both forms have been collected near Keren and also on the shore of Lake Tana (see Note 7, Appendix 1), while the yellow-belly has also been taken on the slopes of Mt. Geech, where on geographical grounds the grey-bellied *poliogastra* (or even *abyssinica*) might have been expected, as will be seen from Map 4.

The other, south-western, grey-bellied form, *omoensis*, is typically represented from the northernmost point of the Omo River (Nono) southwards through the comparatively humid valleys in Jimma and Kaffa to the beginning of the flatter ground at the head of Lake Rudolf. Specimens from north of Nono are more puzzling, Gomit River birds (about fifty miles S.W. of Lake Tana—R. E. Cheesman, *in litt.*) are more like *abyssinica*, yet a bird from further north, on the west shore of the lake (Azobahr) is almost typical *omoensis*. Two more birds from Kunkur, still further to the north and west, are also more like *omoensis* than *abyssinica*, but they have dull upper parts—in other words, they are in this respect intermediate between the two forms, and these birds might be hybrids. But again, the dullness in plumage might be correlated with the fact that their environment is drier than normal for *omoensis* (see Note 8, Appendix 1). However, against both these hypotheses, Dr. Auber finds that the melanization of these dull-looking Kunkur birds is the typical (A) of *omoensis* without infusion of (B). In any case, although *omoensis* and *abyssinica* have not been recorded from the same locality anywhere, Map 4 suggests that round the west of Lake Tana they may overlap considerably; the big gap in the recorded distribution of grey-bellies just south of the Lake might be due to the accidents of collecting—much of the Blue Nile gorge is inaccessible.

On the whole, the ranges of grey-bellied *abyssinica* and *omoensis* and yellow-bellied *senegalensis* do not help to settle their taxonomic relationships. The extent of their geographical overlap and the absence of indubitable hybrids would in most groups of birds suggest specific separation, but in *Zosterops* the South African situation, described subsequently, shows that the ordinary rules do not necessarily apply.

On the east side of the mountains the widely-ranging lowland grey-bellies, *abyssinica*, are, so far as known, strictly allopatric with *omoensis*. This is not recorded east of the Omo Valley, while *abyssinica* is not known west of the Rift. A narrow ridge of highland, occupied by the montane *poliogastra*, intervenes between them. Also on the south of its range *omoensis* appears to be allopatric with the yellow-bellies (*jubaensis*; formerly *smithi*) occupying the arid country from the head of Lake Rudolf eastwards. Further, at least in Ethiopia these yellow-bellies seem allopatric with *abyssinica* on the north, though from lack of collecting it is not certain whether this relationship is maintained eastwards all the way through Somaliland (see Note 9, Appendix 1).

To summarize: in the east and south of Ethiopia *abyssinica*, *jubaensis* and *omoensis* are all allopatric; in the west *abyssinica*, *omoensis* and *senegalensis* all overlap round Lake Tana.

Geographical variations within the lowland forms

The local representatives of *senegalensis* (*sensu stricto*) are typical in colour, but the few specimens available from the Lake Tana–Mt. Geech area are abnormally large, as expected from the altitude. Their wings measure 59, 59 and 60 compared with 52–59 (but mean only 54·6) in the nearest (Sudan) birds at an average of 2,000 ft. lower.

The variation in the southern yellow-belly, *jubaensis* (see also *Bull. Brit. Orn. Club*, **72** : 50–51), is slight and in accord with expectation. Birds from higher altitudes, near Yavello, are a little bigger (wing 53·6) than they are further west, round Lake Rudolf (wing 52·1), or further east towards the Indian Ocean (wing 51·8), and perhaps not quite so dull-plumaged.

In the more widely ranging *abyssinica* the variations are more marked. In the first place, the most northerly birds on the African mainland, from Eritrea and the Red Sea Hills of the Sudan at an average altitude of 3,500 ft., are the smallest, wing 54·4 mm., compared with Abyssinian birds, *ca.* 4,500 ft., average 58·3 and British Somaliland, *ca.* 4,000 ft., average 57·1. All specimens from Abyssinia, Eritrea and the Sudan have brown beaks, a character unknown elsewhere in Africa except in *omoensis*. But all the British Somaliland birds have beaks more or less black. In plumage the northernmost birds tend to be more yellow-green above, not so dull (greyish) as the others.

Two populations of these grey-bellied birds are isolated by water, but both are little differentiated. Across the Red Sea birds of this type occur between about 1,500 and 5,000 ft. from near Mecca (that is, further north than the most northerly occurrence of *Zosterops* in Africa) to the Aden Protectorate, and they have been separated under the name *arabs*. In these birds the carotenoid is further reduced, so that they are even more dingy than Abyssinian *abyssinica*, with no yellow on the head and only slightly whitish lores. Moreover, they share the peculiarity of the brown beak. In dimensions they are extremely close to both Abyssinian and British Somaliland birds—wings 57·5 compared with 58·3 and 57·1 respectively, tail/wing ratio 73·5 compared with 72 and 73·4.

On the " continental " island of Sokotra, off Cape Guardafui, the tip of Somaliland, the birds average slightly brighter (more yellow-green) above than continental birds, though the yellow on the throat is no stronger, and they have little or no yellowish on the forehead. With wings averaging 56·1 and tail/wing ratio 71·8 they are not distinctive in dimensions. The beak is scarcely longer in proportion than in the mainland populations (beak/wing ratio 24·1 compared with 22·9–23·7), but it is interesting that it is not brown but black, like that of its nearest neighbours, in Somaliland. Thus the two isolated populations of *abyssinica*, though named, are " poor races ".

Provisional taxonomic conclusions

(1) The yellow-bellied and the grey-bellied highland birds, *kaffensis* and *poliogastra* are conspecific. It is not worth while to retain the name *schoana* as distinct from *kaffensis*.

(2) The grey-bellied lowland *abyssinica* is conspecific with the yellow-bellied *jubaensis* (*smithi*) and the grey-bellied *omoensis*.

(3) The yellow-bellied bird that enters western Abyssinia from West Africa (*senegalensis*) presumably belongs to a species different from (1), which looks so different, and from (2), which it overlaps.

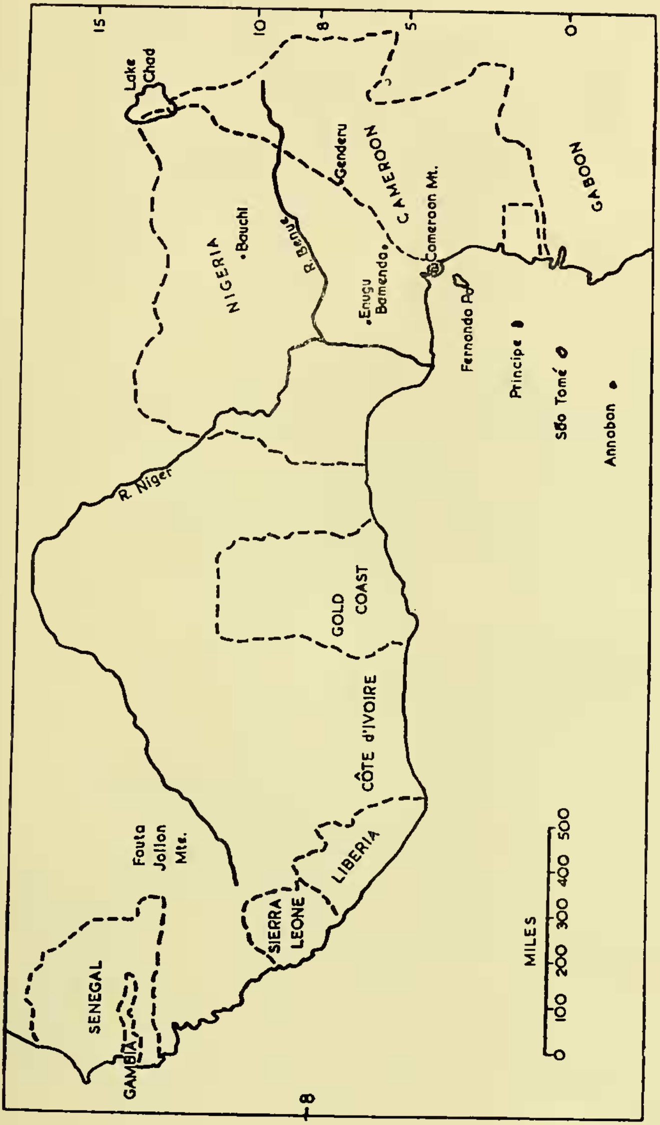
(4) The name *socotrana* is retained, on the character of the black, instead of brown, beak, but the range of the form is extended to include British Somaliland.

REMAINDER OF NORTHERN TROPICAL AFRICA

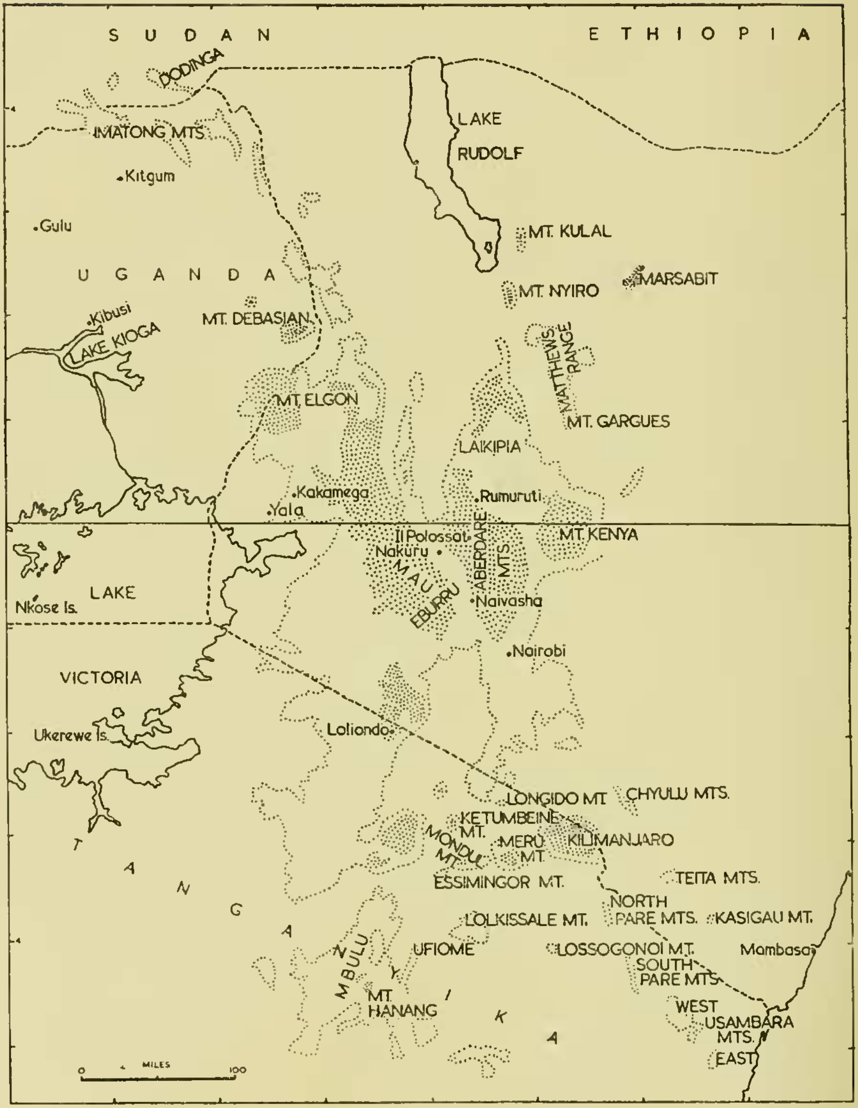
The whole northern savanna belt of Africa, south of about 14° N., is occupied by a brightly coloured *Zosterops* (*senegalensis*) with much yellow pigment and less melanin than any other form in Africa. It extends from the Atlantic (Senegal) almost to the coast of the Red Sea, from which its range is separated by the highlands of Eritrea and Abyssinia (Maps 1 and 4). Southwards the brightly coloured birds extend for an average depth of some five hundred miles towards the Equator with very little variation. Almost the whole of this vast area of nearly two million square miles is lowland, below 3,000 ft. The main exceptions are (*a*) the chain of small detached areas of plateau and mountain at the head of the Gulf of Guinea, (*b*) the Imatong group of mountains on the Sudan–Uganda border, (*c*) the western slopes of the Abyssinian highlands. (There are also the Futa Jalon massif in the west and the Bauchi plateau in eastern Nigeria, from neither of which is any *Zosterops* specimen available.)

The climate is driest in the north—predominantly thorn-bush country, merging southwards into " savanna " (tall grass with small deciduous trees) and ultimately, in the wettest parts, into tropical evergreen forest. The highlands carry some montane forest. In many parts of the area *Zosterops* seem to be uncommon and only about 200 specimens have been available for study.

From east to west through the belts of thorn country and savanna no local differences in plumage can be detected, though there are interesting differences in size (see Appendix 3, populations 13–18). Where, however, the rainfall is higher there are changes in plumage, chiefly connected with increases in melanin. Of the typically yellow *senegalensis* the most westerly representatives, from the Gold Coast to Senegal (Map 5), are the smallest—wing mean 53·5 mm. In Nigeria, the Cameroons and Oubangi-Chari the birds north of about 8° N. are larger, averaging 55·9, but in Southern Nigeria they are not (wings only 53·7). Further east, in the Sudan, birds north of 8° N. are about the same size (56·1) as those in the same latitudes in Nigeria and the Cameroons, but nearer the Equator, in the southern Sudan, extreme north-eastern Belgian Congo and the neighbouring corner of Uganda, they are smaller (54·6), much as in same latitudes in West Africa. As already noted in Part 3, these differences are closely correlated with the minimum temperatures. Then from slightly higher altitudes in the flat country of northern Uganda the few specimens available are a little larger than the foregoing, and finally the eight high-altitude specimens from 5,000–7,000 ft. on the western edge of the Abyssinian plateau



MAP 5. West Africa.



Contour at 4000 ft.

MAP 6. Kenya and Northern Tanganyika.

and on the slopes of the Imatong group (Sudan–Uganda border; Map 6) are, as expected, the largest of all, with wings averaging 59·6 mm.

Apart from birds so much darker that they have received different names (dealt with below), the specimens can be divided into (*a*) the yellowest, (*b*) the greenest, (*c*) intermediates—the whole colour-range being small. The yellowest specimens are scattered through the whole range of *senegalensis*. The greenest birds, which, along with a few of the intermediates, can be matched with exceptionally bright specimens from the savanna belt south of the Equator (*anderssoni*), come from the high eastern localities just mentioned as providing the biggest birds.

Within West Africa the *Zosterops* change more markedly in plumage in the south-west corner, where the rainfall rises rapidly to over 120 inches. From the wet, forest, areas (rainfall over 80 inches, well-distributed) of Sierra Leone, Liberia and Côte d'Ivoire (Abidjan, rainfall 77 inches) all the specimens available are dark and dull, apparently owing to a general increase in melanin—i.e. as expected under Gloger's rule—without strengthening of carotenoid. (These birds have usually been called *leoninus* of Sclater, but as Rand (1951) has pointed out, this is a synonym of *demeryi* of Büttikofer.) These dark birds have wings even shorter (52·8 mm.) than the brighter birds to the north (53·5) and again the minimum temperature (68° F.) is exceptionally high. No detailed evidence is available of transition from the typically yellow *senegalensis* to the greener *demeryi*, though one specimen (" Kamasigi, Sierra Leone ") is intermediate. This lack of evidence is probably because collecting has been sporadic in this part of Africa and the belt of transition from dry country to wet is narrow.

East of the western Côte d'Ivoire, drier country comes right to the coast again until Nigeria is reached. Here dark birds can again be expected, but the present evidence from Nigeria is inconclusive (see Note 10, Appendix 1). Further to the south-east, however, round the Gulf of Guinea, the lowlands, which are exceptionally wet and hot, are occupied by the birds of the expected type (the so-called *pusilla*), small and richly coloured, with plenty of melanin giving them green upper parts and flanks, but also strong, slightly orange-tinged, carotenoid and a golden forehead. With wings 49–53 (mean 51·3), tails 30–33 (mean 31·5), these birds are the smallest in Africa—in accord with the high local minimum temperature, 69° F — and they also have the lowest tail/wing ratio (61) except for the similar neighbouring birds from Manenguba (see below). Birds of this type occupy the southern Cameroons and Gaboon south to at least 1° 45′ S. (Mbigou) and east to at least 16° E. Most of this area receives between 70 and 120 inches of rain, well distributed, and evergreen forest abounds. It is, in fact, on the north-western edge of the great Congo forest; and similar birds probably exist in a narrow belt along the edge of the forest right across the north of the Congo Basin. However, the only skins from this belt, which come from Medje, a thousand miles to the east, though recorded as *pusilla* (Chapin, 1954), differ somewhat—see below—so that if specimens become available from intervening localities they may be expected to show an east–west cline.

At their western end these little " *pusilla* " abut upon the mountainous area along and close to the Nigeria–Cameroons border, with Cameroon Mt. (13,000 ft.) on the shore of the Gulf of Guinea and 100 miles to the north-east the Bamenda–Banso highlands (7,000 ft.), which tail off northwards past Genderu into the flats round Lake Chad. Between Cameroon Mt. and Bamenda smaller isolated highlands occur—Manenguba, Kupe, and the Rumpis. Serle (1950, 1954) has shown that all these highlands are occupied by richly coloured *Zosterops* (with plumage like that of the lowland " *pusilla* "), which have all been called *stenocricota*, a form described from Cameroon Mt. Also in these mountains several *Zosterops* have been collected that are so dull and dark that they have been regarded as a different species (*Z. phyllica*). They appear, however, to be merely cases of individual deficiency in carotenoid (Moreau, 1953).

The specimens from the highest average altitude, 6,000 ft. in the Bamenda–Banso highlands, are the biggest—wing-mean 58·7 mm., tail/wing ratio 65·5. From an average of 4,000 ft. on the Kupe, Manenguba and Rumpi Mts. the birds are much smaller, wing-mean 53·1, tail/wing ratio 58. The birds of Cameroon Mt., which occupy it up to over 9,000 ft., may well be larger at the higher levels, but those specimens labelled with an altitude come from an average height of only 4,000 ft. and average small—wing-mean 54·2 mm., tail/wing ratio 62. Each of these populations has a tail disproportionately short when compared with birds of similar wing-length anywhere else in Africa, as already discussed in Part 3. The biological significance of this peculiarity, localized round the head of the Gulf of Guinea, is unknown.

While the strong melanin of these Cameroon birds, both montane and lowland, is regarded as correlated with the high rainfall, the general appearance of their plumage differs from that of the other dark, high-rainfall, *Zosterops* of West Africa, those of Sierra Leone and Liberia, in being brighter, evidently as a result of stronger carotenoid throughout. The highland birds are indeed so like some on mountains in East Africa that some workers, though not Bates (1930) nor Serle (1950), have regarded them as conspecific and not closely allied to the surrounding *senegalensis*. This conclusion would fit with the remarkable affinity between the montane avifauna of Cameroon Mt. as a whole with that of East Africa. Half the passerines of Cameroon Mt. belong unquestionably to East African species and, though no geographically intervening specimens are known, some of the birds are not even subspecifically distinguishable —see Moreau (1952) for discussion.

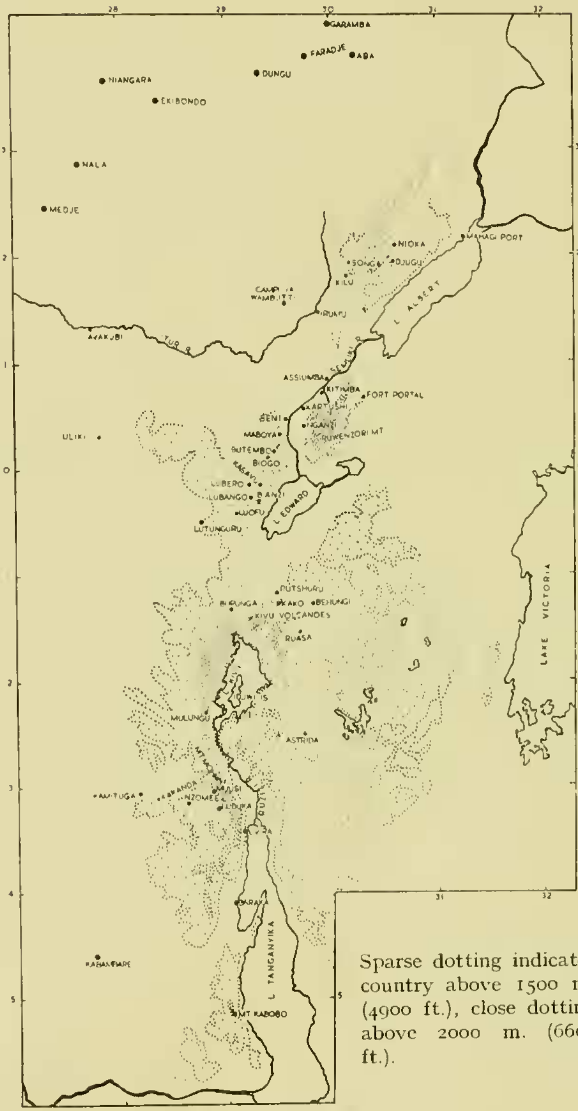
The idea of specially close affinity between *stenocricota* and montane birds elsewhere must, however, be rejected. In the first place, the *Zosterops* (*stenocricota*) of the mountains differ only in size—and that, no doubt, clinally—from the *Zosterops* ("*pusilla*") of the lowland forest at their feet. Actual transition to typical yellow *senegalensis* is shown so far only by three specimens which are intermediate in both colour and tail/wing ratio between *stenocricota* and *senegalensis* ("*genderuensis*" Reichenow), from 100 miles north of the Bamenda highlands, where the country is somewhat lower and drier. Collecting in the lowlands east and west of Bamenda may be expected to yield further intermediate specimens; but owing to the closeness of the isohyets the belt of transition is probably narrow. To the west no specimens are at present known from nearer than Enugu (100 miles away), a savanna locality where the birds are typically yellow *senegalensis*, and to the east the situation is rather similar (see Note 11, Appendix 1).

Cameroon Mt. differs from every other in the African continent in possessing two Zosteropids of undoubtedly different species, for its higher parts are inhabited by both *stenocricota* and the highly aberrant *melanocephala*, which appear fully sympatric and which associate together on the trees (Serle, 1950). With its black and brown plumage, pale beak and general loss of carotenoid, *melanocephala* differs so greatly from all others on the African continent that it has usually been kept in a separate genus, *Speirops*, along with other aberrant birds on the islands in the neighbouring Gulf of Guinea. There also each *Speirops* occurs alongside a more normal *Zosterops*. These are discussed in Part 5 below, and because the situation on Cameroon is so like that on the islands discussion of *melanocephala* will be postponed.

Further east, through the southern zone of the savanna and as far as the north-eastern Belgian Congo and Uganda, typical "yellow" *senegalensis* persist without change of plumage to south of 3° N. There incipient change can be detected. In the Congo (Map 7), while birds from Niangara (3° 35′ N., 27° 50′ E.; in savanna) appear typical, those of Garamba (4° 10′ N., 30° E.) and also Ekibondo (3° 32′N., 28° 24′ E.) are a trifle greener, while at Medje (2° 26′ N., 27° 17′ E.) in a wetter, forest, climate, the birds are much darker. As already noted, they have gone by the same name (*pusilla*) as the equally small birds a thousand miles to the west, but at Medje they are not quite so short-tailed (ratio 65 against 62) and are much less yellow on the forehead. *Zosterops* do not seem to extend further south towards the centre of the Congo Basin (cf. the blank shown on Map 1). Chapin (1954) living for a year at Avakubi, eighty miles nearer to the equator, never recorded a *Zosterops*.

As already noted, in the extreme east of the range of *senegalensis*, on the borders of the Sudan, the birds become greener as they ascend the mountains on the Sudan border (the Imatongs, Didingas and Dongatona). The *Zosterops* associated with the forests on the tops of these mountains have nearly as much melanin as those on the mountains of the Cameroons, though not quite such rich yellow, and are indistinguishable from birds on the mountains round Lake Nyasa, over a thousand miles to the south and on the other side of the equator. This occurrence of "yellow" and "green" *Zosterops* on the same small mountain will be further considered when the more numerous examples in the Nyasa area come to be dealt with. Meanwhile, it seems that the green Imatong birds, like those of the Cameroons highlands, are derived from the surrounding "yellow" *senegalensis* and owe their resemblance to each other and to the Nyasa birds to convergent evolution in similar climates.

South of the Imatongs, in Uganda north of about 1° N. (which is dry), the *Zosterops* are a trifle greener than typical *senegalensis*. It seems certain that this indicates transition to the distinctly greener birds, long known as *stuhlmanni*, in the country with higher and better-distributed rainfall on the northern and western shores of Lake Victoria (Maps 6 and 7). These birds differ in plumage from those of the tops of the Imatongs (and elsewhere) only in a slightly warm tinge, which has been described as "cinnamon". More collecting is needed to establish this transition



Sparse dotting indicates country above 1500 m. (4900 ft.), close dotting above 2000 m. (6600 ft.).

MAP 7. Central Africa.

in Uganda thoroughly (see Note 12, Appendix 1) and some discontinuity may be expected from the long east-and-west barrier interposed by the swamp belt of Lake Kioga and associated waterways. This transition is important in interpreting the taxonomy of the African *Zosterops*, because, as will be shown below, the Lake Victoria birds lead gradually to populations with plumages as richly green as any in Africa.

Summary

Bright yellow *Zosterops* extend from Senegal to the western slope of the Abyssinian plateau. In size they vary consistently with climate and altitude, always averaging larger in higher and/or cooler localities. Wherever the rainfall in the lowlands is such as to give a "forest climate", the birds show more melanin ; but the resultant plumages are slightly different in the four detached wet areas, Sierra Leone—Liberia, head of the Gulf of Guinea, north-eastern Belgian Congo, and southern Uganda. Transition from "yellow" to "green" birds appears to take place in all these cases in a few miles distance, in conformity with rapid change in climate. The two mountain groups that are surrounded by "yellow" *senegalensis*, at the head of the Gulf of Guinea and on the Sudan–Uganda border, are both occupied by larger and greener birds. Here again, transition from the lowland, yellower, type is believed to take place.

It is concluded that (except the aberrant bird of the top of Cameroon Mt.) the whole of the birds considered in this section belong to the same species, *senegalensis* ; the subspecific names that can usefully be applied are *demeryi* for the greener birds of Sierra Leone, *stenocricota* for the greener birds round the head of the Gulf of Guinea and eastwards and *stuhlmanni* for the greener birds on Lake Victoria.

KENYA AND NORTHERN TANGANYIKA TERRITORY

This area (Map 6) differs from all others considered in the number and abrupt isolation of its ecological (montane) islands and, conformably, in the number of its well-marked forms of *Zosterops* (Text-fig. 10) within a small area. The lowland birds have always been regarded as specifically distinct from the highland, which is doubtless correct, and there has been great diversity of opinion about the specific allocation of the highland birds. Essentially, the area consists of dry thorn-bush and "savanna", nearly all with rainfall under 30 inches, out of which rise the Kenya Highlands and an archipelago of smaller highlands, each bearing some montane forest, but effectively isolated from each other by lower, hotter and drier country.

The Kenya Highlands extend about 150 miles each way, at altitudes of at least 5,000 ft., with several parts rising to 10,000 ft. and over. Much montane forest, which has certainly been more continuous in recent historical times, still exists throughout the Kenya Highlands, but they are deeply penetrated by savanna. In particular the Rift Valley past Nakuru and Naivasha is far drier than the mountains on either side ; and although it is narrow and much of its floor is over 5,000 ft. a.s.l., it is something of a barrier for forest organisms.

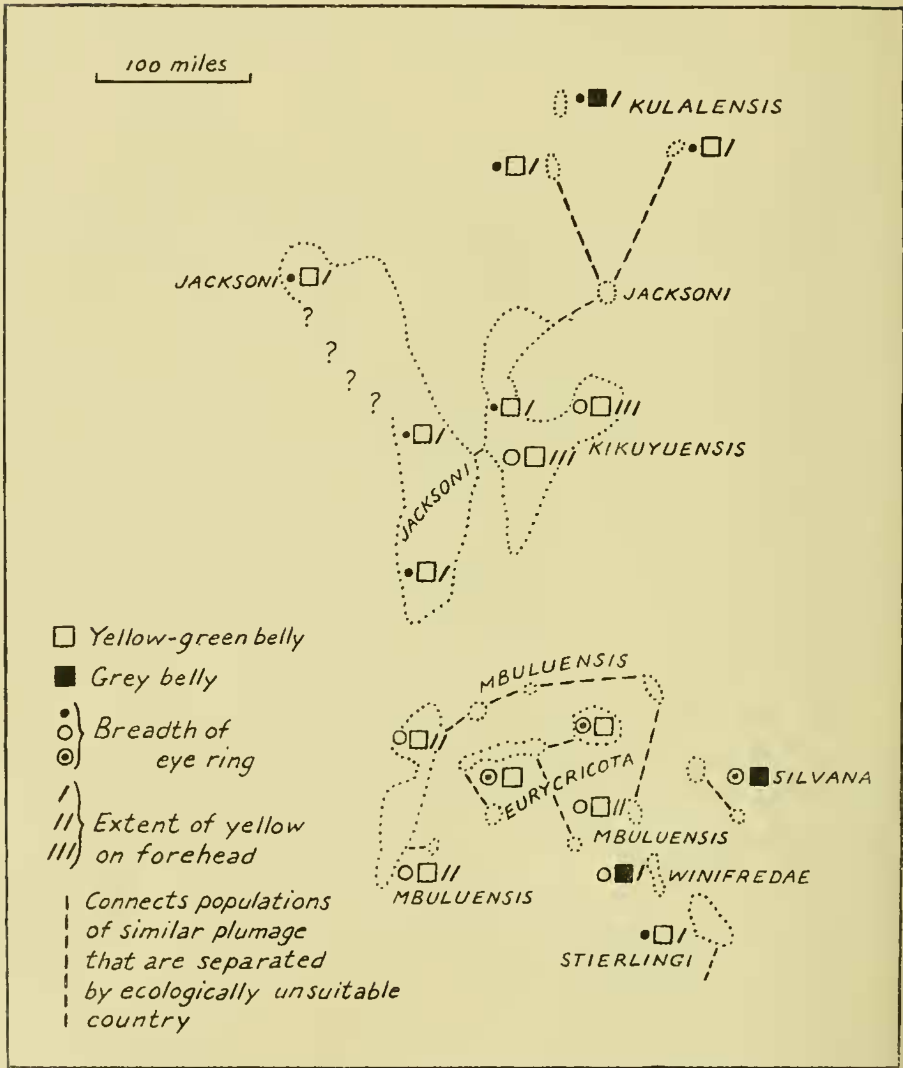


FIG. 10. Geographical distribution of characters in East African *Zosterops*.

The less extensive highlands of East Africa range in size from Kilimanjaro, which rises to nearly 20,000 ft. and carries a great girdle of forest, to Kasigau and Marsabit, each a little over 5,000 ft. with a forest cap, and the anomalous East Usambara plateau, with a forest covering that, thanks to proximity to the Indian Ocean, extends practically down to sea-level.

The dry country separating the various highlands is occupied by a small, rather pale, yellow-bellied *Zosterops* that surrounds all the montane forms. This type of bird is palest and greyest in the north-east, where, on the Abyssinian border, we have already met with it, from Lake Rudolf to the Indian Ocean, under the name *jubaensis*. Further south, down the coast[1] and also inland, birds of this type become slightly greener above (less grey) as the altitude and rainfall increase. Finally, in the neighbourhood of Nairobi and again in Mbulu,where they reach as high as 6,000 ft. a.s.l., these non-forest *Zosterops* (here usually called *flavilateralis*) are birds of yellow-green upper parts and lemon-yellow underparts with some green on the flanks. Even at their brightest and freshest they have, however, a certain "dusty" look, shared by no other yellow-bellied *Zosterops* on the continent. As noted previously, this effect is probably due to the nature of their melanization (B type).

These dry-country birds increase in size with increasing altitude, as expected. The specimens from below 4,000 ft. (average altitude 2,500 ft.) have mean wing-length 54·0 mm., those from higher altitudes (averaging 5,000 ft.), 55·3 mm. It may be added that in this dry habitat the *Zosterops* probably move about a good deal, with corresponding increase in gene-flow.

These savanna *Zosterops* and the montane birds that they surround can hardly be regarded as geographically separated, for on the slopes of the mountains savanna and secondary bush interdigitate with the forest, which, owing to human interference, is nearly everywhere in retreat. Moreover the ecological separation between montane forest and savanna *Zosterops* is not complete, since both are liable to frequent secondary growth and introduced trees. Mr. A. Forbes-Watson *in litt.* has noted that in the Teita Hills at over 5,000 ft. both the local mountain birds (*silvana*) and the savanna birds frequent the same (non-primary) vegetation and that the same species of fruit can be found in the stomachs of both. Actual mixed feeding-parties of highland and lowland *Zosterops* have been noted in a garden near Nairobi (*kikuyuensis* and *flavilateralis*, Mr. J. G. Williams *in litt.*) and in exotic trees in Mbulu (*mbuluensis* and *flavilateralis* in *Grevillea* used as coffee-shade, Dr. G. Zink *in litt.*).

There is no suggestion of hybridization between the two forms and no difficulty in distinguishing the montane birds from those of the surrounding savanna anywhere in Kenya or Northern Tanganyika except in Usambara. There montane and savanna birds begin to converge in appearance, with a consequent problem of differentiation that continues southwards through Tanganyika Territory.

So far as known, all the East African mountains that retain any forest are inhabited by montane *Zosterops* (see Note 14, Appendix 1), even such small and

[1] It appears to be a fact, and one for which no explanation can be offered, that in southern Kenya and all through Tanganyika Territory, *Zosterops* are extremely rare in the comparatively damp coastal strip, the vegetation of which appears to be thoroughly suitable for them (see Note 13, Appendix 1).

isolated mountains as Marsabit and Kasigau. Their differentiation is remarkable for, apart from smaller variations, there are eight forms so unlike in appearance that they have been allocated among five different species. Five of the eight forms occur east of Kilimanjaro, within a space of 250 miles ; and of these five each is within sight of the stations of at least two others. Two of the geographical gaps do not exceed twenty miles. Thus, although the differences between the forms are not so great, the *Zosterops* situation in this ecological archipelago of East Africa is comparable to that of the *rendovae* group, isolated from each other by sea, in the Solomon islands, to which Mayr (1947) has drawn attention.

In the East African montane birds the main variation is in three characters, the distribution of which is shown diagrammatically in Text-fig. 10 :

(*a*) The birds of Kulal in the north, Teita and South Pare (N.E. and S.E. respectively of Kilimanjaro) have grey bellies. All the rest have bellies more or less green and yellow.

(*b*) Eye-rings are biggest in Kilimanjaro and Teita birds, up to 5 mm. broad and covering much of the side of the head ; smaller but still bigger than elsewhere in Africa (up to 3 mm. broad) in the eastern Kenya highlands and in an arc round the north of Kilimanjaro, Mbulu–Chyulu–North Pare ; smallest in the north, northwest and southeast.

(*c*) Golden foreheads are particularly large and rich in the eastern Kenya highlands ; somewhat less marked in Mbulu–Chyulu–North Pare ; entirely absent on Kilimanjaro and Teita ; and intermediate elsewhere.

In Kenya west of the Rift the highlands (above about 6,000 ft.), from Mt. Elgon to Loliondo, are occupied by a large, rather dull-coloured green bird (*jacksoni*) with rather small eye-ring and a yellow forehead that is usually narrow but sharply defined. The carotenoid throughout the plumage is rather "colder", less golden, than that of the other montane *Zosterops* of East Africa. The most northerly birds, those on Elgon, tend to have less sharply-defined foreheads (so that some females look like South African and Nyasaland birds) and to be slightly yellower than those of the main West Kenya Highlands. (But I agree with those who hold that they do not merit the separate name *elgonensis*.) These tendencies, if slightly exaggerated, would produce a bird like those inhabiting the tops of the Imatong group of mountains on the Sudan border (top left-hand corner of Map 6), about 200 miles to the north of Mr. Elgon. This Imatong type is believed to have arisen there by local evolution (see preceding section) and the resemblance is to be borne in mind when considering the classification of the African *Zosterops* as a whole.

Within the western Kenya highlands the size of the birds varies, at least in part as expected from the altitudes. The largest birds (wing 62·0 mm.) are in the centre, between Elgon and Naivasha and including the Mau, at a mean altitude of 8,500 ft. Further south, mean altitude 7,000 ft., wings average only 60·6 mm. Also in the north, from Mt. Elgon itself, the birds are small (wing 60·6), but the few specimens available with altitude data average only 7,000 ft.

It is not certain what relationship the *jacksoni* of the western Kenya Highlands bear to the much yellower *stuhlmanni* of the shores of Lake Victoria, a bird regarded in the preceding section as transitional from the yellow *senegalensis* of West Africa. From Mr. Elgon westwards for at least 100 miles no *Zosterops* seems to be known in collections. However, south of Elgon, from an area less than 100 miles square, mostly at about 4,500–5,000 ft., round Kakamega and the basin of the Yala River, the birds (described by Van Someren as *yalensis*) are brighter than *jacksoni*, with less melanin generally, and are smaller (wing 58·3 compared with 62·0). In their slightly yellower plumage and, in some individuals, less defined yellow on the forehead, the Yala birds show a tendency towards the Lake Victoria birds. No cline is, however, demonstrable because nearly 150 miles intervene between the Yala localities (see Note 15, Appendix 1) and the nearest *stuhlmanni* specimens.

Birds of *jacksoni* type extend east across the Rift Valley in a puzzling fashion, which does not seem to have been realized hitherto. This will be reverted to later. Meanwhile the point to make is that most of the Kenya Highlands east of the Rift are occupied by a strikingly different bird, *kikuyuensis*, one of the most showy *Zosterops* in Africa, with very large golden patch on the forehead and a broad white eye-ring. Apart from the usual larger size at higher levels, the Mt. Kenya birds are indistinguishable from those further south, to beyond Nairobi, and from the Aberdares (see Note 16, Appendix 1). It is unfortunate that the various specimens in collections labelled "Aberdares" bear no precise localities or altitudes, because somewhere towards the north end of the range there seems to be contact with birds of *jacksoni* type, and it is important to know what their relations are.

Typical *jacksoni* come right to the wooded western edge of the Rift Valley, including the Eburru spur, which projects just north of Lake Naivasha to within ten miles of the east side of the Rift (there formed by the western foot of the Aberdares). From this side of the Rift various collections possess birds of *jacksoni* type labelled Naivasha, Il Polossat (at 7,000 ft. about fifty miles north of Naivasha), Rumuruti and Laikipia. These localities are all on the northern end of the massif of which the Aberdares form the crest and the local *jacksoni* appear to be separated by no ecological barrier from the Aberdares *kikuyuensis*. In particular, the forest at Il Polossat is "mixed, with juniper, just the same as on the Aberdares" (J. G. Williams *in litt.*). Are then these birds allopatric? In any case the distances involved are very small and there is no sign of intergradation or hybridization between these two very different forms of *Zosterops*, both of which are essentially highland.

The eastern birds of *jacksoni* type themselves form part of an interesting series. All the seven specimens from the area Naivasha–Rumuruti are a trifle yellower than typical *jacksoni*, but they are equally large. Sixty miles to the north-east, across a belt of dry thorn-bush, rather similar birds reappear on Gargues Mt. (about 8,800 ft.), the southern end of the Matthews Range, but they are smaller (four average 59·6 against 62·0) and also duller, with a trifle less of both melanin and carotenoid. These birds may or may not extend along the whole seventy miles of the Matthews Range; but on Mt. Nyiro (about 9,000 ft.), just detached from the northern end, the birds are slightly different. They are of the same "difficult", generalized, type but rather larger than the Gargues birds and very variable in plumage. The seven Nyiro birds available average 62·5 mm. in wing compared with 59·6 in the Gargues. In plumage the Nyiro birds range from almost typical *jacksoni* to markedly duller and paler, like those of Gargues. (It is difficult to understand why Jackson and Sclater (1938) attributed Nyiro and Orr Valley specimens to the Abyssinian subspecies *kaffensis*, which has the carotenoid more golden and the forehead brighter and more defined.)

To the east across eighty miles of thorn-bush, the *jacksoni* type of bird reappears, still further "attenuated", on the small volcano Marsabit, which rises to only 5,500 ft. The forest is of a very dry type, with much *Juniperus*, and the rainfall exceptionally low for any sort of evergreen forest—only 32 inches at the meteorological station 1,000 ft. below the summit. Twelve Marsabit birds are all dull-coloured and markedly small (wing 57·5)—but still quite different from the *jubaensis* (yet smaller and of a "dusty" pallor) of the surrounding thorn-bush. Thus we have a west-to-east cline of decreasing pigment and size on the three highlands, Laikipia–Gargues (Matthews Range)–Marsabit, all strongly isolated.

As noted, the birds of Mt. Nyiro, off the north end of the Matthews Range, do not conform with the Laikipia–Marsabit trend: they are larger and not so dull-coloured. Their tendency in these respects is towards the *Zosterops* (*kulalensis*—see Note 17, Appendix 1) of the forest belt on Mt. Kulal (7,700 ft.), an old volcano forty miles to the north and also isolated by very dry country. The available specimens (from 6,000–6,500 ft.) have the same wing-average, 62·5, as the Nyiro birds, but they are grey-bellied and perhaps also have rather longer tails and beaks. In other respects they resemble the Nyiro birds more closely than any others (and particularly than any of the Abyssinian birds, the nearest montane neighbours to the north). This situation finds an almost exact parallel in the relationship (described below) between the grey-bellied *winifredae* of the South Pare mountains and the yellow-bellied birds of the Usambaras a few miles to the south. And in fact morphologically the Kulal birds are to the South Pare birds just as the Nyiro are to the Usambara. The first two mentioned, which there is no reason to regard as closely related, show the same degree of convergence as the second pair.

Reverting to the main eastern Kenya islands, for about 150 miles south from the southern end of *kikuyuensis*, near Nairobi, no montane *Zosterops* is known. Then, in the neighbourhood of Kilimanjaro and the Tanganyika border there are a number of forms. Birds resembling *kikuyuensis* in their broad eye-rings, but with less marked golden foreheads and less green on the underparts, appear in an arc of small mountains surrounding Kilimanjaro on the north, from the Mbulu Highlands and Mt. Hanang on the west, through Ketumbeine, Longido and the Chyulus to the North Pare Mts. (*mbuluensis*)—see Note 18, Appendix 1. A typical *mbuluensis* is known also from Essimingor Mt., of which more later. The very variable birds from the two extreme stations, Mbulu and North Pare, cannot, in series, be distinguished in plumage. (The fact that the latter average a little smaller, wing 60·4 compared with 62·5, is presumably at least in part because they come from altitudes averaging 1,000 ft. lower.) Yet between them intervenes Kilimanjaro, with a very distinctive *Zosterops*—*eurycricota*, with the largest size of eye-ring (up to 5 mm. broad), completely green forehead in nearly all specimens and, as a rule, much deep green and no bright yellow on the underparts. The difference between typical *eurycricota* and typical *mbuluensis* is striking, but individual variation is such that slight overlap occurs in each of the characters mentioned.

Z. eurycricota extends westwards from Kilimanjaro, wherever there is forest, along the highland that connects Mt. Meru and Mondul Mt. with Essimingor, which is separated from Mbulu only by the twenty-five miles of the Rift Valley. Two specimens from Essimingor are exactly like Kilimanjaro birds, yet the third specimen known from this small mountain is the equally typical *mbuluensis* already mentioned. It is difficult to know how to interpret this. It could mean that *eurycricota* and *mbuluensis* belong to different species ; but perhaps the *mbuluensis* is a straggler from across the Rift Valley. A good sample of the Essimingor population is needed, especially as a basis of comparison for the future, in case one type of *Zosterops* is here replacing another.

Birds like those of Kilimanjaro reappear in the attenuated forest on Lolkissale Mt. and the edge of the Lossogonoi plateau, fifty miles south of Kilimanjaro and cut off by arid thorn-bush. The only difference is that most of the Lossogonoi and Lolkissale specimens have a slight golden wash on the forehead, a feature that is very rare in the Kilimanjaro–Meru–Mondul population.

About fifty miles east of Kilimanjaro, across, as it were, the Mbulu–Chyulu–North Pare arc, the grey-bellied birds of the Teita Hills (*silvana*) resemble the Kilimanjaro birds in their very large eye-rings and otherwise entirely green heads. Also they share with them the highest tail/wing ratio in East Africa, over 78. They differ in having a higher beak/wing ratio and more melanin generally—enough to make their throat greenish rather than yellowish—and a bright yellow edge to the "bend of the wing". This contrasts so sharply with the green of the rest of the upper parts that it is conspicuous in the field (M. E. W. North, *in litt.*) and at first strikes one as a peculiar feature. It is, however, only an exaggeration of the tendency, visible in a few *eurycricota*, for the tiny feathers on the bend of the wing to be slightly yellower than their neighbours. On the whole the Teita birds are undoubtedly more closely related to the Kilimanjaro than to any others.

The Teita form is of special interest because it exists in exceptionally small numbers for a continental *Zosterops*. Fortunately for its survival, it is not entirely dependent on the few hundred acres of primary evergreen forest that remain in the patches. It has been observed in secondary *Albizzia–Gummifera–Combretum* woodland in the mountains, in flocks alongside, but not mingling with, flocks of the yellow savanna bird, *flavilateralis* (A. Forbes Watson, *in litt.*), and stomachs of both birds contained the same food. M. E. W. North estimates that the total population of *silvana* throughout the Teitas may be under 2,000 ; but similar birds inhabit the little cap of forest on Kasigau Mt., over fifty miles to the east and separated by arid thorn-bush.

These grey-bellied Teita birds are only fifty miles from the Pare Mts. On the north end of this chain the yellow-bellied *mbuluensis* occurs, as already mentioned. Further south, the middle of the chain is lower and probably too dry for montane *Zosterops*, but towards the southern end, after an interval of some forty miles, montane forest reappears and is there inhabited by the last of the three grey-bellied birds of East Africa, *winifredae*. Apart from the belly-colour, these birds are rather intermediate between their northern neighbours, in North Pare, and their southern neighbours in the mountain forests of Usambara less than twenty miles away across the semi-desert Mkomasi gap. This might be due to clinal environmental influences of some sort, or, in view of the small distances, to gene-flow from both directions. The South Pare birds have carotenoid less golden than the North Pare, less prominent yellow on the forehead and tail/wing ratio lower—73 compared with 75. All these differences are tendencies towards the Usambara birds, which have slightly smaller eye-rings, less rich coloration and tail/wing ratio only 69. This Usambara type of bird extends down through Tanganyika Territory nearly to the Zambesi, and is further discussed in the section "Southern Tropical Africa". It is remarkable that on the East Usambara Mts., where evergreen forest extends down the seaward slope nearly to sea-level, the montane *Zosterops* in question stops at the edge of the plateau, at about 3,000 ft. Incidentally, no "savanna" *Zosterops* has been found round this seaward foot of the mountains or on the neighbouring coastal plain.

Summary and classification

Zosterops show sharper differentiation in this area than in any other. But among the montane forms extent of differentiation is not related to the extent of existing ecological barriers.

The three grey-bellied forms each appear to be more closely allied to their nearest yellow-bellied neighbours than to any other *Zosterops* and not to be specifically distinct from them.

On the same highland, at the north end of the Aberdares, *jacksoni* (from the west) and *kikuyuensis* (from the south) appear to meet allopatrically, without ecological barriers and without hybridization. This could mean that they belong to different species. The same applies to the occurrence of both *mbuluensis* and *eurycricota* on Essimingor but, partly because these forms show some overlap in characters, a different view is preferred.

Apart from the belly-colour of the South Pare birds, the four montane populations of Usambara, South Pare, North Pare and Kilimanjaro, at first sight very dissimilar, form a (discontinuous) series of increasing pigmentation and size of eye-ring. This would suggest conspecificity (and the Usambara and Kilimanjaro birds, which look so different, have identical songs—see Appendix 2). Also, with *mbuluensis* as link, the Kilimanjaro *eurycricota* can be regarded as conspecific with the East Kenya *kikuyuensis*.

Certain difficulties have now to be faced. The Usambara birds, just regarded as conspecific with the Kilimanjaro, are, as will be argued below, conspecific with the *stuhlmanni* of Lake Victoria. These are believed to intergrade, through the Yala population, with *jacksoni*. It follows that *jacksoni* would be conspecific with *kikuyuensis*, although, as noted above, the Aberdares situation suggests that they are not. A possible explanation is that here, as in the Great Tits, *Parus major*, of eastern Asia and other examples (Mayr, 1947), we have a meeting of branches of the same species so long separated as to be genetically incompatible.

On the whole, I am prepared to treat all the montane *Zosterops* as conspecific, retaining the names *kulalensis, jacksoni* (to cover the whole discontinuous cline from the West Kenya highlands through Laipikia and Gargues to Marsabit and Nyiro), *kikuyuensis* (East Kenya highlands), *silvana* (Teita), *mbuluensis* (including *chyuluensis*, for the arc Mbulu–North Pare), *eurycricota* (Kilimanjaro and outliers), *winifredae* (North Pare), *stierlingi* (Usambara ; see next section). The lowland birds, specifically distinct, are *flavilateralis*, intergrading with *jubaensis* (conspecific with *abyssinica*).

CENTRAL AFRICA

The area dealt with here is a highly mountainous strip about two hundred miles by six hundred, between 38° and 31° E., 3° N. and 6° S., on the eastern edge of the Congo Basin (see Map 7). Here the *Zosterops* show a wide range of variation in size and in general colour of plumage but not in eye-ring, forehead or belly colour. Although they include some of the deepest green birds in Africa, I regard them all as conspecific with the yellow West African *senegalensis*, which in the preceding section was traced south nearly to the Equator.

Zosterops appear to be absent from the centre of the Congo basin 2° N.–5° S., cf. Chapin (1954), but are widespread in the east of it. Topographically this strip is dominated by the western (Albertine) Rift Valley and associated mountains, with the following main features, in succession from north to south : Lake Albert, Ruwenzori (17,000 ft.), Lake Edward, the Kivu volcanos (with forest belts up to over 10,000 ft.), Lake Kivu (at about 5,500ft.), Lake Tanganyika (at about 2,600 ft.). From north-west of Lake Edward to near the head of Lake Tanganyika the highland is continuous at 5,000 ft. or more, but Ruwenzori is isolated from this by the few miles of lower and drier country round Lake Edward. The highlands north-west of Lake Albert are more isolated (and the local *Zosterops* are so little represented in collections that they cannot be discussed). On their west side the Central African highlands decline rapidly into the fully lowland conditions of the Congo Basin with its equatorial forest climate. On the east, however, all the country southwards from Lake Albert, through Uganda and past the shores of Lake Victoria into Tanganyika Territory, lies at nearly 4,000 ft. or over.

In almost the whole of this strip of Central Africa except the flats round Lake Albert the rainfall approaches 60 inches and considerable areas west of Lake Kivu and north-west of Lake Tanganyika, some below 3,000ft., receive over 80 inches. The wettest areas of all are the forested mountains, of which the chief are Ruwenzori and the Kivu volcanos.[1] The vegetation and appearance of the whole area have been graphically described, with photographs, by Chapin (1932).

As previously stated, in Uganda the "yellow" *Zosterops senegalensis* appears to develop into the greener *stuhlmanni* as it approaches the shores of Lake Victoria.

[1] To the very local high humidity of these mountains the isohyets in Bultot (1950) probably do not do justice.

Here it is a common bird wherever there are trees, at least from about Jinja round the northern and western shores of the lake and thence across western Uganda (but no *Zosterops* seems to have been collected on the other, drier, half of the lake shore). The plumage of *stuhlmanni* is again of a very generalized type—diffuse yellow forehead, medium eye-ring, greenish flanks contrasting with yellow centre of underparts. In fact the only feature that distinguishes these birds from those which are widespread on the mountains of Nyasaland and Tanganyika (and also the Imatong group on the Sudan border) is a certain warm tinge throughout the plumage. Uganda birds from between about 3,700 and 5,000 ft. have wings averaging 58·1, tail/wing ratio 71, dimensions which, like the plumage, are not distinctive.

The *Zosterops* populations of islands in Lake Victoria would repay investigation. The only series is one of twelve kindly obtained for me by Mr. E. G. Rowe on Ukerewe Island, in the south-west of the lake (see Map 6). They have about the same-sized wing (58·8) as the mainland birds just described, but a higher tail-ratio (75), the Ukerewe eye-ring is larger, and the slightly warm tinge is absent from the plumage. In fact, lacking this tinge, in plumage the Ukerewe birds are separable from Imatong mountain birds—and indeed from birds on mountains round Lake Nyasa—only by slightly bigger eye-rings. Again, from Nkosi Is., the most exposed of the Sesse group in the north-west corner of the lake (see Map 7), which is known to have faunal peculiarities (see Pitman, 1929), the single *Zosterops* available has a wing 4 mm. longer than that of any specimen from the opposite mainland and also an abnormally yellow head.

Westwards these *stuhlmanni* extend to the wetter Ruwenzori massif, occupied by *Zosterops* up to at least 9,000 ft., and also to the low hot banks of Lake Albert. Between, there is a narrow corridor, mostly below about 3,000 ft., occupied by the Bwamba forest country (see van Someren and van Someren, 1949), leading north-west across the Semliki into the forested country of the upper Ituri, which declines to about 2,000 ft. In this highly diversified country on the western edge of *stuhlmanni* there is, as would be expected, much variation in *Zosterops*, which has been the subject of great differences in taxonomic opinion. There are adequate series only from Ruwenzori itself and from the upper Ituri (Stockholm Museum) and it is particularly unfortunate that no specimens seem to be known from localities linking the Ituri with the Ekibondo–Garamba area (already referred to under *senegalensis* as showing incipient divergence from that type) and with the smaller and more heavily pigmented birds at Medje, 150 miles to the north and the W.N.W. respectively.

Eighteen birds are available from Bwamba and the low forest country to the west, from Kampi ya Wambuti to Beni, eighty miles to the south, which includes the type-locality of *toroensis*, Kitimba (which is not in present-day Toro). They are, as expected, all small, mean of wings 53·7, tails 36·9.[1] Also as expected, the birds are strongly pigmented, with plenty of both melanin and carotenoid, but they have little yellow on the forehead. On the whole they resemble the Medje birds more

[1] As Chapin (1954 : 187) has noted, at Nganzi, near Beni, at 3,900 ft. at the western foot of Ruwenzori, he got a male with wing 61 alongside birds of *toroensis* size. The large bird might have been a straggler from the higher slopes.

than any others and probably they intergrade with them over the intervening "uncollected" country. The Bwamba birds appear to be transitional between those of Uganda on the east (*stuhlmanni*) and the Ituri birds on the west (see Note 19, Appendix 1).

There has been much difference of taxonomic opinion also about the Ruwenzori birds. I find that specimens from above 5,000 ft. (averaging 6,900 ft.) tend to have a little more melanin in the plumage and to be a little longer in wing and especially in tail than Uganda birds (altitude 4,000 ft.) to the east—wings 56–63 (mean 60·2) against 55–62·5 (mean 58·1), tails 41–49 (mean 44·5) against 37–44 (mean 41·3). (For the Ruwenzori mountain birds some authors have used the name *scotti*.) A series from the western foothills at Mutsora, 4,000 ft., averages the same size as Uganda birds at the same altitude on the east.

In plumage both the higher-altitude Ruwenzori birds and those from the western foothills average a little darker than the Ituri birds (*toroensis*) and also than the Uganda birds. But the Ruwenzori population, with its generally strong melanin and "warm" carotenoid, cannot be separated in plumage from most of the slightly larger birds of Kivu (see below), a hundred miles to the south, on the other side of Lake Edward. In both the Kivu and Ruwenzori populations many of the birds have the melanin of the flanks extending towards the centre and clouding the whole underparts (as in *virens* of South Africa). This does not happen in Uganda birds, but at the same time there are individuals from the mountains that cannot be distinguished in plumage from Ituri or Uganda individuals.

The identity between Kivu and Ruwenzori birds is noteworthy because the birds of the highlands just west of Lake Edward (see also Prigogine, 1953), which form an almost continuous connection above the 1,500 m. contour (approx. 5,000 ft.) between Ruwenzori and Kivu, differ slightly in being purer green, without the "warm" tinge. Moreover within the small area of these highlands, only some fifty miles by seventy, there is striking variation in size of *Zosterops* with altitude. Birds from Lutunguru, on the western edge of the highland, and other localities between 1,400 and 1,500 m. (average 4,700 ft.) have mean of wing 57·1, tail 40·6, while birds from 1,600–2,700 m. (average 6,800 ft.) have wing 61·5, tail 46·6. Moreover the tail/wing ratio of the latter birds is 75 against only 71 for the former series—in accordance with the trend throughout the continent, cf. Part 3. A similar change in dimensions, correlated with altitude, takes place in the Kivu District. Birds from the volcanos average longer-winged and, more markedly, longer-tailed (62·5, 47·9) than those from nearer lake-level (60·9, 45·4).

South-west of Lake Kivu and north-west of Lake Tanganyika lies an area highest in the east, dipping west into the Congo Basin at Kamituga, pioneered by Grauer but recently worked most usefully by Dr. A. Prigogine. The *Zosterops* (described as *reichenowi* Dubois) differ from those of the Lutunguru area, 150 miles to the north, only in having slightly more melanin (perhaps connected with the higher rainfall, 80 against 60 inches). Like them, *reichenowi* lacks the warm tinge characteristic of Ruwenzori and most Kivu birds (as well as *stuhlmanni*) and indeed seems to have less carotenoid than any of the populations mentioned. It may be that further exploration will show a continuous narrow belt of these "colder"-coloured *Zosterops* by-passing the Kivu population on the west (as adumbrated by the fact that Mulungu birds are a trifle greener) and intergrading with the small richly coloured birds of Bwamba–Ituri further north.

The main interest of these southern birds, from Kamituga eastwards, which are all alike in plumage, is the change in their dimensions with altitude in a very short distance. The high-level birds, round about 7,000 ft., in the Muusi neighbourhood, are practically the same size as those at 6,800 ft. in the highlands west of Lake Edward—wings averaging 61·4, tails 45·3. But only forty miles to the west, round Kakanda–Kulundu, at 4,000 ft., the averages drop to 55·9 and 39·1 ; and twenty miles west again, round Kamituga and Utu, at about 3000 ft. (here the floor of the Congo Basin), the birds are smaller still, with wings only 53·1, tails 35·5. Further, a few geographically intermediate specimens fall perfectly on this size-cline.

Summary

While all the birds are regarded as conspecific with *senegalensis*, it seems worth while to retain the name *toroensis* for the small lowland birds N.W. of Ruwenzori and *reichenowi* for the " cold " green birds of the area N.W. of Lake Tanganyika. Ruwenzori and Kivu mountain birds are regarded as transitional between *stuhlmanni* of Uganda and *reichenowi*. Local variation in dimensions is great but consistent. It cannot be recognized nomenclatorially.

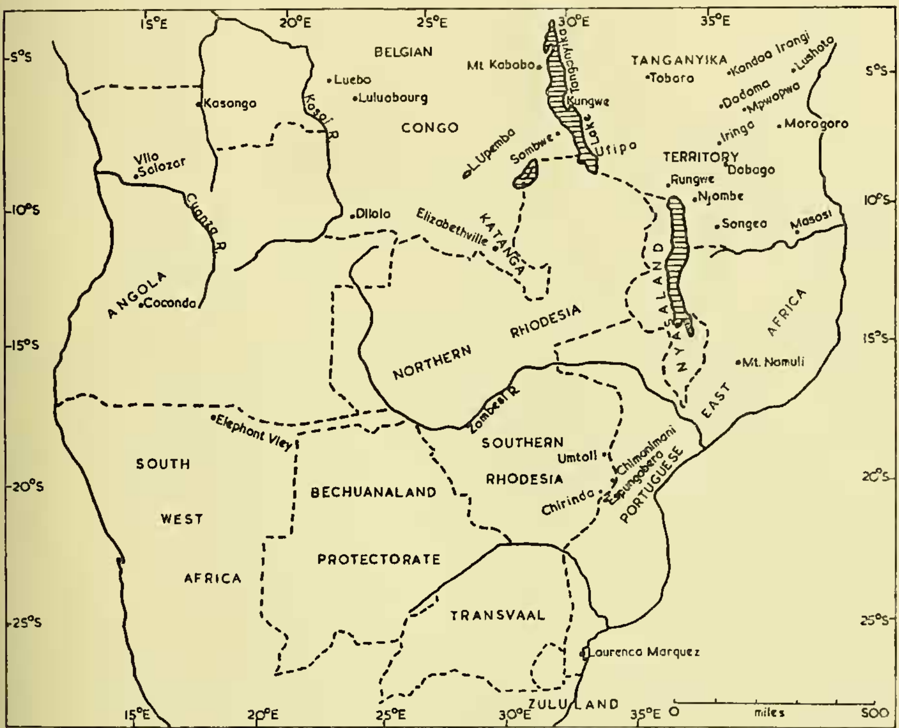
SOUTHERN TROPICAL AFRICA

This area (Map 8) extends from the southern limits of those dealt with in previous sections to the borders of South Africa. It contains a number of poorly differentiated *Zosterops* populations which differ in little but intensity of melanin, but have been allocated to one or other of two species on this criterion.

I believe that this distinction cannot be maintained except for the lowland, dry-country form, *flavilateralis*, which extends south from Kenya, in a strip through the middle of Tanganyika to about as far as the line Tabora–Morogoro. Between Tabora and Lake Victoria *Zosterops* seem to be absent ; and in southern Tanganyika *Zosterops* appear to be purely montane except for rare occurrences in the south-east (see Note 13, Appendix 1).

The material of *flavilateralis* from Tanganyika does not suffice to define the local variation fully, but specimens from the moister country of Kondoa, Morogoro (Uluguru) and Usambara tend to be particularly green. They show in fact so much convergence towards the highland (forest-edge) birds of Uluguru and Usambara that some skins are not at first sight easy to allocate—even though the *flavilateralis* prove to have (B) melanization and the montane birds (A). The possibility of hybridization, for example at Lushoto (4,000 ft., Usambara) and Kibungo (700 ft. eastern foot of Ulugurus) whence particularly " difficult " skins come, cannot be excluded. However, I believe the best course is to regard these highland and lowland forms as belonging to different species.

Turning now to the Congo Basin, it appears, as already noted, that as far south as about 5° S. no *Zosterops* have been collected in the space of nearly 400 miles, between Luluabourg (in the Kasai country of the south-west) and the foot-hills of the mountains overlooking Lake Tanganyika in the east, or, to the south-west, Upemba (Map 8). But between the Kasai and the Transvaal, and from Angola to



MAP 8. Southern Tropical Africa.

the Indian Ocean, *Zosterops* with variable, but never highly distinctive, features are generally distributed. Some of them cannot be differentiated from the birds of the Imatong group of mountains far away on the Sudan–Uganda border, others differ from birds on the north and west of Lake Victoria only in slightly less "warmth" of tone, others again can be matched by abnormal West African individuals, others are extremely like the richly pigmented birds of Kivu and still others cannot be separated on plumage from individual South African birds.

Taken as a whole, these southern tropical birds range in general colour of plumage from predominantly yellow to predominantly green, and as there is a complete gradation the attempt to divide the populations between the species on this criterion alone, as is usually done, leads to difficulty. In dimensions all the populations, irrespective of colour, form one group of tail/wing ratios and beak/wing ratios (Text-figs. 4 and 8) and also when tail/wing ratios are plotted against altitude and against minimum temperatures (Text-figs. 6 and 7). (In the whole group of populations the tail/wing ratio is unusually constant in the face of changes in altitude and temperature, and so is the beak-length with changing wing-length.) The main point for the taxonomist is that analyses of dimensions give no support to the view that more than one species of *Zosterops* is present in the area under discussion. This view meets, however, with some difficulties on geographical and ecological grounds.

Dark populations are always, and dark individuals are nearly always, found at higher altitudes and where evergreen forest occurs, while the yellower birds usually occur in drier and lower country, dominated by deciduous woodland. But this ecological distinction is far from invariable. For example, R. H. Smithers has noted (*in litt.*) yellow birds in Southern Rhodesia in both "thorn veld" and evergreen growth, and Benson (1946*a*) has obtained such birds in the evergreen forest at Vumba (near Umtali, 5,000 ft.). Swynnerton, as his labels show, has collected yellow birds in the Chirinda and Chipete forests, but a dark bird in the Chimanimani evergreen bush half-way between these two localities. Again, some individuals on the border of Northern Rhodesia and the south-eastern Congo (Katanga) are so green that some workers have allocated them to *virens* (see Note 20, Appendix 1)—there are no mountains in the area, but some patches of evergreen growth too extensive to be called riparian (C. W. Benson *in litt.*). One is reminded of the dark individuals, formerly regarded as a separate form, *phyllica*, that crop up in the Bamenda highlands (see p. 354).

Lynes (1933) collected both yellower and greener birds (which he attributed to different species) in the same situations, the "edges of the forest-jungles" at 6,500 ft. in the Njombe District of Tanganyika Territory. Moreover, the *Zosterops* of the Kungwe–Mahari mountains, on the east shore of Lake Tanganyika, are associated with evergreen forest (about 6,000 ft. upwards), yet when laid out with a long series of specimens from southern tropical Africa they fall into the yellower half. In Nyasaland the relict forest on some mountain tops (Mangoche, Dedza, Chongoni and Nchisi) is occupied by birds as yellow as those of the Rhodesian savannas, but greener birds occupy Mlanje, Cholo, Soche, Zomba, Ndirande and (greenest of all) Nyankhowa and the Nyika Plateau (Benson, 1945, 1953). No adequate meteorological data exist, but Benson (*in litt.*) is satisfied from his local experience that the mountains of the first group have a lower rainfall than the others. In none of the mountain forests where green birds have been collected has it been proved that a transition from yellower to greener birds takes place as the mountain is ascended and evergreen forest becomes the dominant vegetation ; and there seems no proof that yellow and green birds associate together. There is in fact no indication of such local clinal variation as previously noted on the slopes of the Imatong mountain group and elsewhere over more level country with a rapidly changing rainfall, as in Sierra

Leone. The Nyasaland situation suggests at first the possibility that here we have ecological replacement of one species by another as in the instances given by Moreau (1948). For example, an isolated mountain forest, from which the typical montane woodpeckers (*Mesopicos* and *Campethera*) are absent, is inhabited by a species of *Yungipicus* that elsewhere is a savanna bird. Moreover, as will be shown in the next section ("South Africa"), a few hundred miles to the south-east of Nyasaland, in Zululand and southern Portuguese East Africa, yellow birds that are undoubtedly conspecific with, and have a distribution continuous with, those of Nyasaland appear to live as "good species" alongside, but ecologically separated from, green South African birds.

These last closely resemble some of the darkest Nyasaland birds in plumage, but they differ from the Zululand yellow birds and from all the Nyasaland birds, both the yellow and the green, in having a higher tail/wing ratio, 75 against 67–71. Here we come up against the question of the value of this ratio as a taxonomic character (Part 3). On the other hand, as noted above, the yellow and the green birds of Nyasaland (and elsewhere in southern tropical Africa) do not differ in bodily proportions. It is a curious fact, however, that the dark birds tend to be unexpectedly small for the altitudes at which they are found. In particular, the dark Nyasaland birds (No. 64 in Appendix 3) have the same mean wing-length, 58·5 mm., as the local yellow birds (No. 63), with an average altitude 2,000 ft. lower and a climate certainly warmer. This is, of course, contrary to the trend otherwise general throughout Africa—and beyond—as discussed in Part 3.

Thus arguments can be adduced for regarding the yellower and the greener birds in at least part of southern tropical Africa as belonging to two different species. Against this are the complete gradation that can be made up from birds from different localities and the fact that Benson (1953), who has an unrivalled knowledge of both forms in Nyasaland, can find no difference in their habits and their calls. On the whole it seems preferable to regard all the *Zosterops* of southern tropical Africa as belonging to the same species.

The most north-westerly population in southern tropical Africa, namely, that in the Kasai district of the south-western Belgian Congo (*kasaica*), is the most distinctive. They are the first *Zosterops* encountered after crossing the great forest from the north. The series from about 4° 30′ S., round Luebo and Luluabourg, consists of very small short-tailed birds (wing 52·5, tail 35·1), which conforms with their low altitude (*ca.* 2,000 ft. a.s.l.) and high minimum temperature (64° F.). On the whole they are more like the little Medje birds 700 miles away to the north-east, on the other side of the Congo Basin, than any others in Africa, but they are rather more olive throughout, with very narrow eye-rings and no clear yellow on the forehead at all. They occupy country that, with an annual rainfall around 60 inches, is not so wet as that of Medje, but nevertheless the resemblance between these two populations, sundered by the forest, may be due to convergent evolution in similar equable climates, rather than to recent common ancestry. It is possible that a narrow belt of small birds remains to be discovered running eastwards from Luluabourg along the southern edge of the Congo Forest to intergrade clinally with the equally small, but greener, birds known from Kamituga (referred to in the section on Central Africa) at the foot of the eastern rim—themselves probably intergrading clinally to Medje.

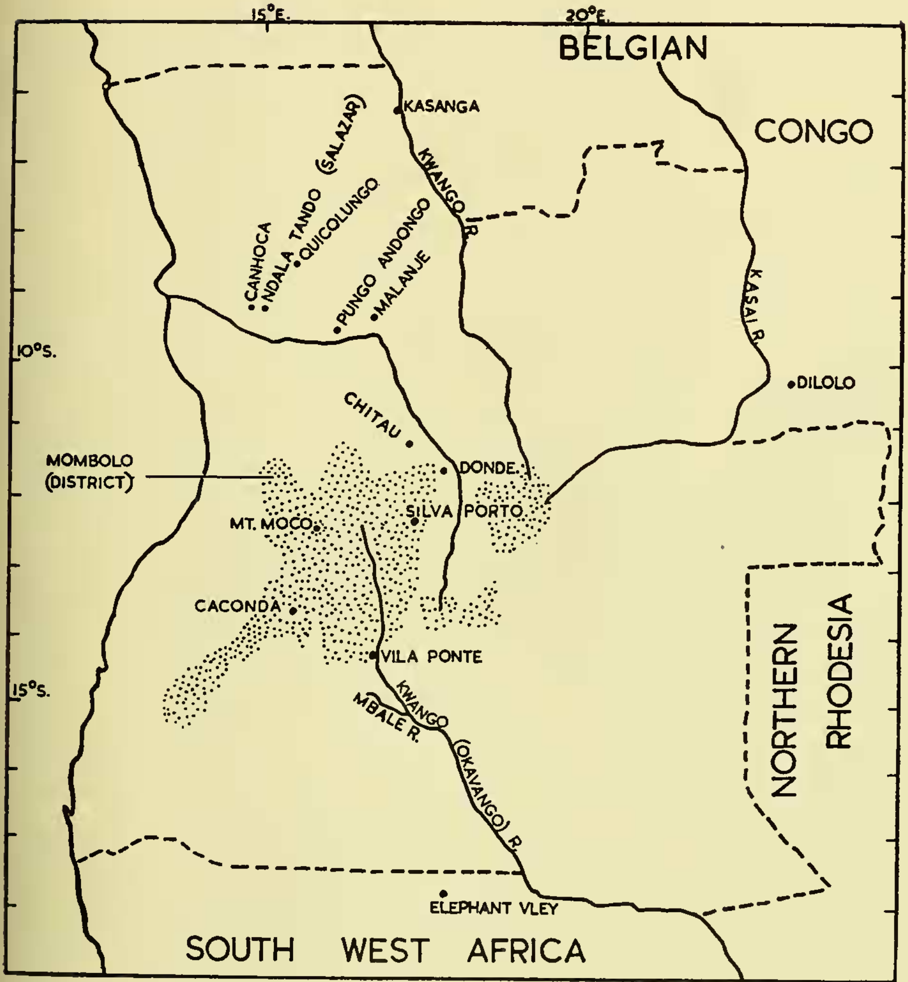
Towards the south-west, *kasaica* apparently extends at least to the north-eastern border of Angola—cf. the one imperfect specimen from Kasanga on the Kwango (Cuango) river. Thence, there is almost certainly intergradation with the birds of the highlands in the centre of Angola, which are much larger and much duller in plumage. The few specimens available from the intervening area Ndala Tando (= Vila Salazar)–Quicolungo–Canhoca (see Map 9), which is rather higher and drier country than that inhabited by *kasaica*, are already duller in plumage and much larger (wing 57·2, tail 39·0).

Another 150 miles intervene to the south before another series of *Zosterops* is available from central Angola (Benguela Highlands) at 4,500 ft. upwards (Note 21, Appendix 3). This area has the highest rainfall in Angola[1] and it is therefore unexpected that the birds there (described as *quanzae*) are all duller in plumage than the Vila Salazar series. This may be connected with the fact that the Vila Salazar area is one of semi-evergreen forest (dominants *Albizzia*, *Celtis* and *Ficus* spp.), while the Benguela highlands, though having a higher rainfall, are occupied by savanna with much (deciduous) *Brachystegia* (Gossweiler and Mendonça, 1939), and with evergreen forest only in gullies (C. M. N. White *in litt.*).

Also, the birds of the Benguela highlands are much larger (wing 61·8) than those round Vila Salazar and in fact are the largest in southern tropical Africa (see Nos. 56 *et seq.* in Appendix 3), although they come from an average altitude of only 5,500 ft. The explanation is presumably that, as data from ten local meteorological stations show, these birds experience abnormally low minima, averaging only 45° F. in the cool season—cf. the general size/temperature regression in Part 3. These large pale birds extend south-east at least to Vila Ponte (wing 64), but further down the Cubango (Rio Mbale) a specimen, though pale, is within the Rhodesian size-range (wing 58).

Further collecting may bridge the present gap in *Zosterops* distribution in this part of Africa—nearly 400 miles to Dilolo in the east and 200 to Elephant Vley in the south—and show whether, as expected, there is a transition to the rather yellower and smaller birds (*anderssoni*) that occupy so much of the remainder of southern tropical Africa. There is at present no evidence that any such *Zosterops* occur further west in Angola, to the Atlantic, or further south in South West Africa, except along the northern border, or in Bechuanaland, but very similar birds are distributed through the Rhodesias, Nyasaland and Portuguese East Africa, right to the Indian Ocean, and also northwards in the south-eastern Belgian Congo to at least 8° S. The whole of this great area is, as already indicated, dominated by

[1] Cf. the isohyets in the *Atlas de Portugal Ultramarino* (Lisboa, 1948). They differ much in detail from those in Gossweiler and Mendonça (1939), but since they are presumably based on more data they are taken to be more nearly correct. As so often in climatological maps, the isohyets have had to be sketched in the Atlas from the records of widely scattered stations and it seems that in drawing them advantage has not been taken of the guidance orography can give. However, the main trends of the isohyets are no doubt somewhere near the truth.



Areas above 1,500 m. dotted.

Map 9. Angola.

deciduous woodland, though patches of evergreen forest occur, especially on the highest points.

The yellowest populations of all are the most westerly, in western Northern Rhodesia. Equally yellow individuals occur as far east as Nyasaland (even at 6,000 ft. on the Nyika plateau), but most of the specimens from east of about 29° E. are a trifle greener than those from further west. The most easterly of all, in southern Portuguese East Africa (Mozambique), Zululand and the low-veld of the north-eastern Transvaal average a trifle greener still. Northwards through Portuguese East Africa it appears that the *Zosterops* generally become a trifle more richly pigmented, especially golden, a character that is best marked (but still only visible when series are compared) in the birds of the Songea highlands on the north-east side of Lake Nyasa. As the single bird collected between there and Indian Ocean, in the lowlands at Masasi, shows the same character, it may be that there is a continuous, though extremely sparse, population over much of south-eastern Tanganyika Territory. These brightly coloured birds of south-eastern Tanganyika can, however, be matched by individuals from Nyasaland and Northern Rhodesia. Whether such birds extend far enough north to come in contact with the pale *flavilateralis*, hitherto not recorded south of the line Morogoro–Tabora, is unknown : and it would be interesting to know their relationships if they do so.

In size the "yellow" populations of the Rhodesias, Nyasaland and also the south-eastern Congo, all around 4,000 ft., are remarkably constant, varying only from 58·6 to 59·9 mm. in average wing and from 39·8 to 42·0 in tail (Nos. 59, 60, 62, 63 in Appendix 3). A series from around 5,800 ft. in N. Rhodesia (No. 61) averages, as expected, larger (wing 61 mm., tail 42·5). By contrast, but again in accord with expectation, the birds from the coastal belt (below 1,000 ft.) along the Indian Ocean average only 56·6 mm. in wing and 39·2 in tail (No. 65).

Returning to Northern Rhodesia, the variation in the *Zosterops* may now be traced north through the south-eastern Belgian Congo (Katanga). About 200 miles north of the territorial border, in the wooded savanna of the Upemba National Park (*ca.* 8° S. ; altitudes 4,500 ft.–6,000 ft.) the birds are duller, apparently with a little more melanin and a little less carotenoid. In this they resemble the birds from the central Angola highlands (in fact Verheyen (1953) has used the same name, *quanzae*, for them), but they are smaller—wing 59·9 against 61·8. Similar populations occur on the west shore of Lake Tanganyika at Sambwe and Kabobo, the latter rather darker. Although there are great gaps east and west of Upemba, from which no specimens are known, it appears that we have a cline from the yellower birds (*anderssoni*) of the Rhodesias and Katanga, northwards through a stage deficient in both pigments to the deep green birds, with much melanin, in the highlands north-west of Lake Tanganyika (*reichenowi*—see section on " Central Africa "). It is curious that, as already mentioned, on the Kungwe mountains just across Lake Tanganyika the *Zosterops* are decidedly yellow.

Turning now to the dark birds, the most richly pigmented of all are those inhabiting the Rungwe and Poroto Mts. at the north end of Lake Nyasa (see Note 22, Appendix 3), a small area that, with one station registering 100 inches a year, is about the wettest in southern tropical Africa. A few miles to the south, on the Nyika, Nyankhowa and Masuku Mts. of northern Nyasaland, the birds are nearly as richly coloured, with dark green flanks contrasting with the strong yellow centre of the underparts; but on the other Nyasaland mountains, further to the south, none of the birds are so deeply pigmented and, as already noted, some are actually yellow.

Facing the Poroto birds on the west, over 100 miles away across the Rukwa depression, the nearest montane *Zosterops* are those of the Ufipa highlands, and they, like those of the Kungwe–Mahari Mts., further north up the east side of Lake Tanganyika, are, as mentioned above, yellower. But eastwards and northwards from Rungwe the highlands are continuous to Njombe and Iringa, and all the *Zosterops* are dark, with a local variation that has greatly bothered taxonomists. It now appears that the birds on the average darkest, and most nearly resembling those of Rungwe, come from round Dabaga, on the top of the humid Uzungwe scarp that forms the seaward edge of the Iringa highlands. The birds that average next darkest are those of Njombe, while those from Iringa itself, which is not so high and humid as Dabaga and Njombe, are a little yellower. (For the nomenclatorial difficulties concerned see Note 23, Appendix 3.)

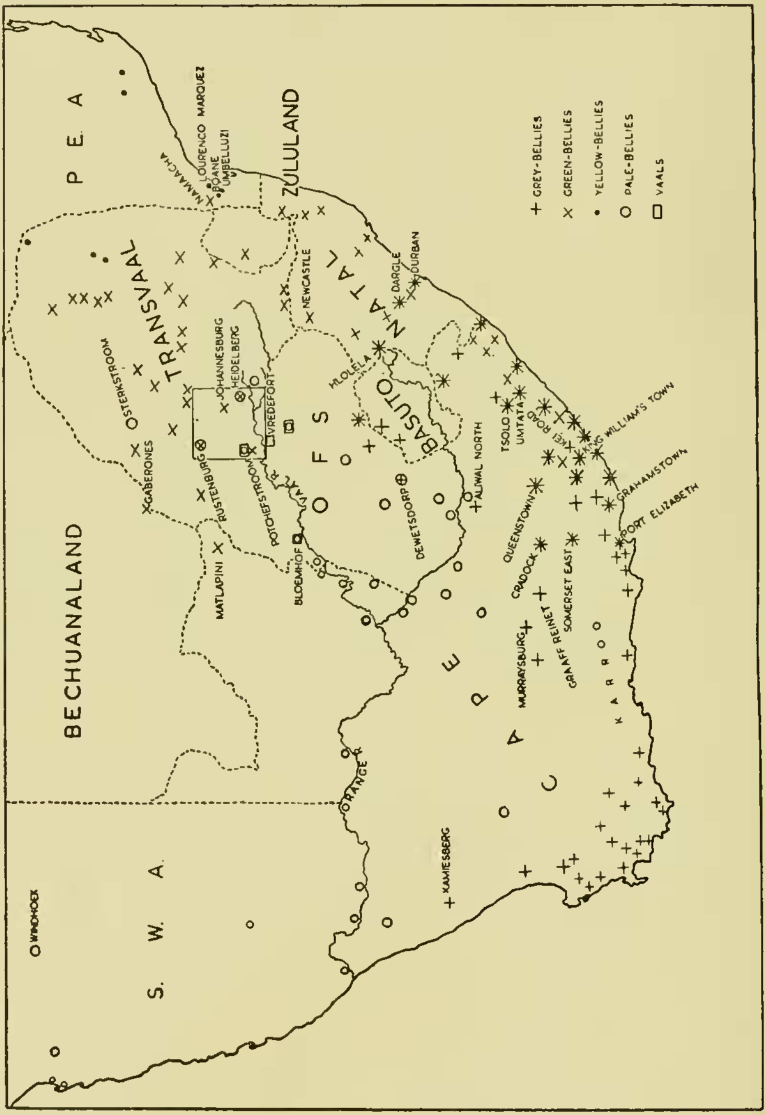
Birds coloured like those of Iringa occupy the isolated mountains further north—Kiboriani, the Ngurus, Ulugurus and Usambaras—getting smaller as the altitude and latitude decrease and the minimum temperatures rise (populations 68–72, Appendix 3). As previously noted, the *Zosterops* of these Tanganyika mountains are partly islanded in the small, generally paler, *Zosterops* of the surrounding savanna which tend to converge in colour. These lowland birds to some extent penetrate the highlands—for example, reaching at least 4,000 ft. in the cultivated areas in the middle of the West Usambara plateau—but there is no evidence that the highland birds ever enter the lowland savanna.

Summary

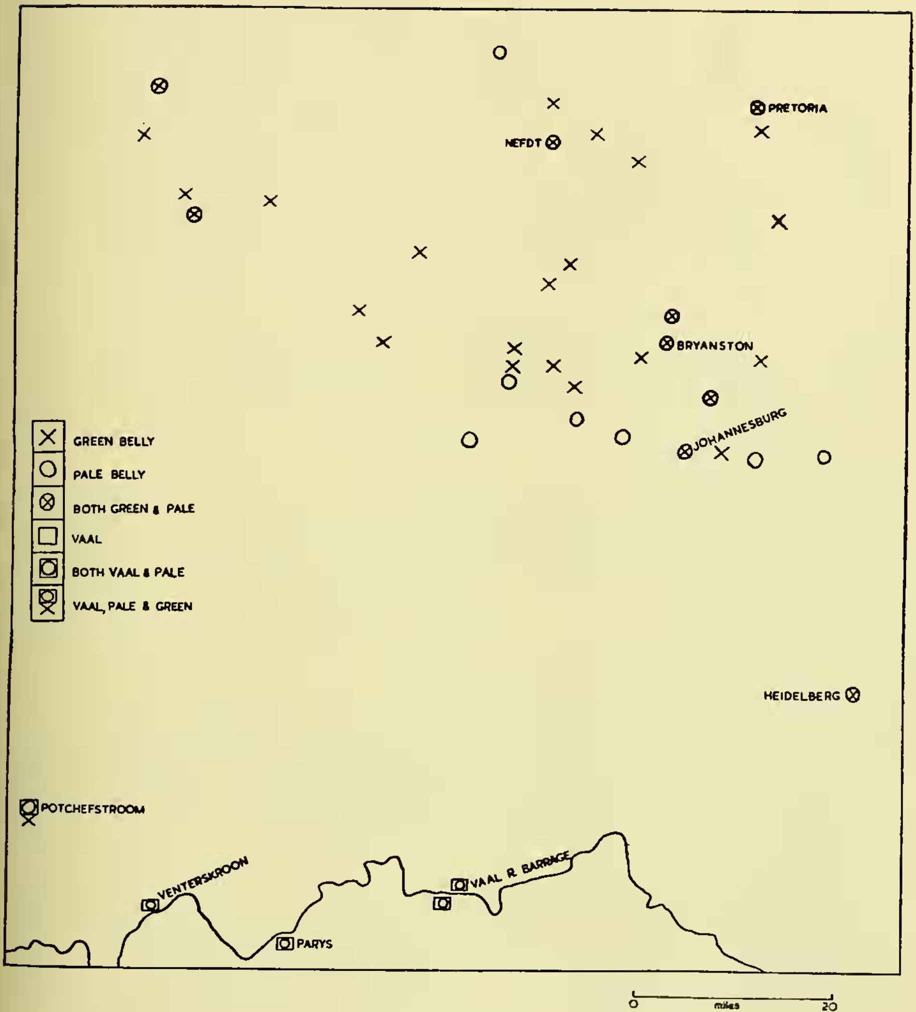
The whole of the *Zosterops* inhabiting southern tropical Africa are regarded as belonging to the same species, *senegalensis*. It may be useful to retain the following subspecific names: *kasaica* for the small olive birds of the south-west Belgian Congo; *quanzae* for the large dull birds of Central Angola; *anderssoni* for the yellow birds from Northern Rhodesia to the Indian Ocean; and *stierlingi* for the more richly pigmented birds of the Nyasaland and Tanganyika highlands. But the ranges of the last three cannot satisfactorily be delimited because intermediate populations are so prevalent and similar birds appear discontinuously, perhaps as a climatic response (convergence).

SOUTH AFRICA

It would have been impossible to write even the present tentative account without much co-operation from ornithologists in South Africa, where I am especially indebted to Mr. C. J. Skead for the Cape Province data and to Dr. R. M. Harwin for mapping the Transvaal situation.



MAP 10. *Zosterops* distribution in South Africa.



MAP 11. *Zosterops* distribution in the southern Transvaal.

South of the Zambesi there are five main colour-forms of *Zosterops*, which have always been regarded as belonging to at least four different species. Their ranges and main characters are given in Maps 10 and 11 and Table 2 (see also Note 24, Appendix 1). For clarity the five forms are referred to in this discussion as "grey-bellies," "pale-bellies", "Vaals", "green-bellies" and "yellow-bellies". Briefly, grey-bellies differ from green-bellies only in lacking yellow pigment on the belly, but from pale bellies in deeper pigmentation of upper as well as under parts and in other characters. Vaals differ from pale-bellies only in having yellow throughout their underparts. Green-bellies differ from yellow-bellies (the *anderssoni* already discussed under "Southern Tropical Africa") in having more melanin throughout and individuals of them can be matched in colour with birds from the mountains of Nyasaland. All the purely South African forms have a high tail/wing ratio (75–79), contrasting with under 70 for the yellow-belly (*anderssoni*) that enters from the north.

TABLE 2.—*The main Characters and Distribution of South African* Zosterops.

N.B.—The subspecific names usually applied are inserted in brackets.

	Belly colour.	Main area.	Upper parts.
(1)	Grey (*capensis*[1] and *atmorii*) . .	Cape Province and Basutoland .	Green
(2)	Whitish with chestnut wash on flanks (*pallida*)	Orange River Basin .	Paler and greyer
(3)	Pale yellow with chestnut wash on flanks (*vaalensis*)	Along lower Vaal R. (all localities shared with *pallida*) .	As (2)
(4)	Green, yellowish in middle (*virens*) .	Eastern Cape, Natal, Zululand, Transvaal .	As (1)
(5)	Yellow, green wash on flanks (*anderssoni*)	Zululand and N.E. Transvaal (thence northwards) .	Yellower than (1)–(4)

[1] The most westerly grey-bellies (" *capensis* ") differ from all the others in this table in lacking any yellow over the lores (or over base of upper mandible).

In South Africa the *Zosterops* arrangement differs from that elsewhere in Africa in that the colour-forms show considerable geographical overlap and even more ecological. All are limited to places where there are trees ; but, given that essential, they show a breadth of habitat tolerance that is unusual in African birds and is great enough to make it difficult to be sure what their original vegetational associations were.

(*a*) The grey-bellies occur from sea-level to over 7,000 ft. (Drakensberg). They inhabit all sorts of tree-growth, from the patches in the extremely dry Kamiesberg (south-east of the mouth of the Orange River) to the Knysna and Hogsback evergreen forests, including gardens and plantations of pine and eucalyptus (Skead).

(*b*) Green-bellies are usually referred to as predominantly forest birds but, with as big an altitude-range as the grey-bellies and a wider geographical range, they inhabit if anything an even greater variety of arboreal vegetation—the coastal forests of the Eastern Cape, Natal and Zululand, the acacia-veld of the Natal uplands, the dry Transvaal high-veld, the gardens of Johannesburg and even the taller " bush " in the east of the Bechuanaland Protectorate.

(*c*) Yellow-bellies are limited to the " low-veld ", the deciduous and pyrophytic " bush " of the eastern Transvaal, Zululand, and Portuguese East Africa, thence spreading north and west across the Rhodesias.

(*d*) Pale-bellies inhabit the southern half of South West Africa, the south-western Transvaal, the northern Cape and the whole of the Orange Free State—much of their area averaging less than 10 inches of rain a year. In the driest parts the birds seem to occur only in the valleys (especially along the Orange River), where there is some water, artificial or other (but there is no record of the birds drinking).

(*e*) Vaal *Zosterops* are known only from localities on and near a short stretch of the lower Vaal River, from all of which pale-bellies are also known.

As will be seen from Map 6, while *Zosterops* are generally distributed in South Africa, there are two areas where they seem at most very sporadic, (i) a wide belt in the western Cape Province from the Karroo northwards and (ii) most of South West Africa and the Bechuanaland Protectorate. The necessary trees exist scattered over much of the second area, but not in the Karroo.

Local Variation

Size generally

As shown in Appendix 3 (populations 73–80), in each colour-type wings average longer in the cooler and/or higher areas, except that the green-bellies of the Natal–Cape lowlands average no larger than the Zululand birds that inhabit a slightly warmer climate (but by only about 2° F.).

Grey-bellies

East of about Port Elizabeth the grey-bellies average slightly yellower on the upper parts and throat and have some yellow on the forehead and lores. (This last feature corresponds with the amount of yellow on the heads of the green-belly population with which they interbreed—see below.) Enough specimens are not available, but the transition from the western form (*capensis*) to the slightly yellower eastern form (*atmorii*) appears to take place in a zone including Murraysburg, Graaff Reinet and Port Elizabeth, from all of which the specimens are intermediate in character.

Well to the north-west of any other specimens of *capensis* two from the dry Kamiesberg are slightly duller above than other *capensis* and have flanks slightly redder. Both these features of their plumage adumbrate the characters of the pale-bellies, which are known from about seventy miles away on the north. However, something similar is shown by northern representatives of *atmorii*, further to the east, near Aliwal North (kindly communicated by Mr. P. A. Clancey). The plumage of these birds (and of one from Dewetsdorp) is duller throughout than that of the *atmorii* nearer the coast. On the flanks, however, these birds are a particularly pure grey, with no reddish, so that they can hardly owe their general divergence from typical *atmorii* to an infusion of the local pale-belly characters. On the contrary, the dullness of the plumage appears to be correlated with the drier climate, for Dr. Auber has ascertained that a Kamiesberg *capensis* contains a lower proportion of (A) melanin and more (B) than a specimen from the more humid Knysna (see Part 2).

Green-bellies

These show much individual variation. Exceptionally dull specimens are scattered throughout the range, but every specimen from the driest part of the range (western Transvaal and eastern Bechuanaland—Note 25, Appendix 1) is slightly pale and dull, with the same divergence from the typical appearance as mentioned above for the dry-country representatives of *capensis* and *atmorii*. Moreover, the dull specimen (from Rustenburg) that has been tested shows a predominance of (B) melanin in contrast to the predominance of (A) melanin in a specimen from a humid Natal habitat (Dr. Auber).

Pale-bellies

Apart from size, no consistent local variation can be established, but the individual variation is very high. Besides occasional faint suffusion of yellow on the underparts, some specimens have the whole area between throat and vent nearly white, others almost entirely rufous. One from near Rustenburg, on the edge of the pale-belly range and some 250 miles from the nearest grey-bellies, has the underparts so grey that it would, if found south of the Orange River, probably have been cited as a hybrid *atmorii* × *pallida*. The occurrence of such a specimen, which must be of pure pale-belly stock, is important to bear in mind when considering another highly abnormal bird, shot at Dewetsdorp in the Orange Free State out of a flock composed partly of grey-bellies. This individual (Kaffrarian Mus. B2863) is predominantly warm russet below, becoming almost grey on the chest—a putative hybrid (see also Note 26, Appendix 1).

General

It will be observed that each of the colour-forms of extensive range in South Africa varies geographically in the same way. Each has its largest individuals in the coolest areas and its dry-country outliers less saturated in colour than the main populations in less arid climates. It is noteworthy that this consistent agreement with Bergmann's and Gloger's rules takes place within what are generally accepted as individual subspecies ; and the agreement with Gloger's holds good in the actual type of melanization so far as this has been tested.

Overlap and Relationships of the Colour-forms

Grey-bellies and green-bellies

As shown in Map 10, there is a great overlap in the geographical distribution of these birds and, as already mentioned, no distinction in their habitat-preferences (or other behaviour). Some information (collated by Mr. Skead) is also available about their relative abundance in different localities. It can be only in general terms because colour of belly is difficult to see in such small restless birds and a formal census in an area where both occur is impossible.

In the narrow belt about King William's Town, where grey- and green-bellies commonly interbreed (see below), they appear to be about equal in numbers. Westwards green-bellies diminish rapidly: at Queenstown, Somerset East and Cradock they are much in the minority, at Grahamstown and Port Elizabeth (less than 150 miles from King William's Town) they are rare, and further west they are unknown. East of King William's Town the grey-bellies at first fall off rapidly, and green-bellies predominate heavily around Butterworth, Tsolo and Umtata, but further north, at the higher altitudes, in and on the borders of Basutoland, the two forms seem equally common again. Thus grey-bellies reassert themselves, as it were, in Basutoland and on the Natal slopes of the Drakensberg after apparently being somewhat eclipsed by green-bellies nearer the coast on the south. In coastal Natal greys are rare, being known only from two specimens (Dargle and Durban—nearly 400 miles east of King William's Town). It is difficult to interpret these occurrences. The Durban specimen is too small to be a wanderer from the Basutoland population and, if a straggler, must have come along the coast from the south-west.

Since Mr. Skead's field observations first suggested the relationships between the grey-bellies and the green-bellies he and his helpers have tried to record belly colour in every case of birds with nests or dependent young. The following results are all derived from the area King William's Town–Kei Road, where the two forms are constantly seen in the closest association:

(1) Grey + green sharing incubation (of 3 eggs later destroyed).
(2) Grey + green with fledglings (belly-colour not ascertainable).
(3) Grey + green feeding one grey fledgling.
(4) Grey + green with one grey fledgling.
(5) Grey + green feeding three green nestlings.
(6) Grey + green ,, three grey fledglings.
(7) Green + green ,, three grey fledglings.
(8) Green + green with three green fledglings.
(9) Green + ? feeding three grey fledglings.
(10) Green + ? ,, grey fledglings (? number).
(11) Green + ? ,, one green fledgling.

(In cases (9), (10) and (11) the second parent was not observed.)

The above data are somewhat conflicting and the record that each bird, both parent and fledgling, is a typical green-belly or a typical grey-belly must be accepted subject to the fact that, as noted in Part 2, only a proportion of intermediates is obvious to the eye. (Indeed this happens even in field observations on the Carrion and Hoodie Crows—Mayr, 1947.) One "good" example of an intermediate *Zosterops* has recently been collected by Skead; its definitely grey flanks are separated by as marked yellow down the middle of the belly as ever occurs in the green-flanked type. Two other specimens from King William's Town and Newcastle have the flanks so dull greyish a green that they look somewhat intermediate.

One definite conclusion from the field data given above is that the two green-bellied parents in (7) must have been heterozygous and that their fertility was normal, but no other genetical inferences can safely be drawn. Nor is the taxonomic problem settled. Bearing in mind also the geographical distribution, it seems that the grey-bellies and the green-bellies cannot be merely colour-phases. If the belt of inter-breeding of the two colour-types is really as narrow as that covered by the limited field-observations, then there might be a case for treating the two birds as species analogous to the Carrion and Hoodie Crows, but on the whole for the present they are best regarded as subspecifically related.

Pale-bellies and grey-bellies

Pale-bellies differ from the other South African *Zosterops* in having less saturated coloration—grey-green upper parts, paler yellow and wholly (B) melanin—presumably correlated with their drier environment. Their beaks tend to be more slender towards the tip, and in voice they differ slightly from both grey-bellies and green-bellies, which are alike. More important, their dimensions are peculiar in that their wings are abnormally short in relation to the low temperatures they experience (Part 3), though they share the high tail/wing ratio of other South African *Zosterops*.

As will be seen from Map 10, in most of the area where pale-bellies and grey-bellies might be expected to overlap, i.e. in the south-western Cape Province, *Zosterops* of any sort have been very little recorded. The two forms have been collected together in only one locality, Dewetsdorp in the Orange Free State (out of the same flock ; Kaffrarian Museum), and the two specimens concerned each show a slight approach to the plumage characters of the other. The only other locality where the two forms have been found close together is Aliwal North (7 miles apart ; Mr. P. A. Clancey). As already noted, all the most northerly grey-bellies—those nearest to the pale-belly range—diverge slightly from the typical in the direction of pale-belly characters, but they can hardly be accepted as hybrids. Moreover, colour is not the only character separating the two types.

Pale-bellies and Vaals

Vaals are known only from the banks of the last 200 miles of the Vaal River and up to about thirty miles on either side (at Potchefstroom, Vredefort and perhaps Heidelberg), in localities where pale-bellies are recorded at the same season of the year, and mixed flocks are reported. The area has no notable ecological peculiarities (Dr. E. A. C. L. E. Schelpe *in litt.*). The relative abundance of the two forms would be impossible to assess reliably in the field. No biological information has been recorded about Vaals except by Plowes (1946 and *in litt.*) ; and it may be doubted whether any significant differences exist.

Vaals have always been regarded as a distinct species (*Z. vaalensis*), but the five I have examined (only six specimens seem to exist in museums) show only one consistent difference from pale-bellies—they have a strong suffusion of yellow all over the underparts, which gives them a brighter yellow throat and a yellow belly with an isabelline, rather than a chestnut, wash on the flanks. Bearing in mind also the geography, specific separation seems unjustified and this is clinched by the existence of somewhat intermediate specimens. Two with slight yellow wash on a portion of the underparts come from Venterskroon and Bloemhof (Transvaal Museum) and one with yellow wash over the whole underparts from Rustenberg—100 miles from the Vaal.

On the whole it seems best to regard "*vaalensis*" as a localized xanthochroic variety of *pallida*. Comparable cases are known. For example, the grass-warbler *Cisticola juncidis*, which has a vast range, from Spain to Australia and Natal, produces in a few square miles at the north end of Pemba Island, and apparently nowhere else, an erythristic form that interbreeds with typical birds (Pakenham, 1937).

Pale-bellies and green-bellies

These two forms overlap in the southern Transvaal to the extent shown in Map 11. Critical information as to the extent to which they associate together in flocks, or interbreed, is lacking, but at Bryanston and at Hartebeestepoort both have been found in the breeding season. North of a line through Johannesburg greens occur, and apparently predominate, right into the dry country of the west, at least to Gaberones, over the Bechuanaland border, and the sources of the Great Marico, with one locality of pale-bellies interpolated—Sterkstroom (Transvaal Museum). The furthest extension of green-bellies south-westwards is at Potchefstroom, where both pale-bellies and Vaals also occur. There is no indication of inter-breeding anywhere.

Green-bellies and yellow-bellies

At the northern end of their range the green birds from South Africa overlap the yellow birds of southern tropical Africa (*anderssoni*) in Zululand and the adjacent north-eastern Transvaal. This is the only case in South Africa where there is evidence of decisive ecological separation between two forms. In Zululand the green birds are said to be confined to patches of evergreen forest in the coastal acacia "bush" and to the forest on the Lebombo Hills (which do not exceed about 2,000 ft.), while the yellows occupy the surrounding more open vegetation (Mr. J. Vincent *in litt.*). It would be interesting to know whether the yellows and greens actually meet or associate anywhere, as, for example, the grey-bellies and green-bellies do constantly in the Cape Province.

All the Zululand specimens available are either typical yellows or typical greens; and it is important to remember that there is a difference in dimensions as well as in amount of melanin. The yellows average about 3 mm. shorter in wing than the greens and their tail/wing ratio is only 69 compared with 75 in the greens (and 75–79 in all other South African *Zosterops*).

From Portuguese East Africa also both yellows and greens have been reported by Dr. A. A. Pinto (1953) and through his kindness I have been able to examine good series, supplemented by ecological data supplied by him. The only typical green ones are from three localities:

(*a*) Namaacha, on the northern extension of the Lebombo Range, at about

2,300 ft., where patches of evergreen forest occur—conditions exactly like those in which green birds occur in Zululand.

(*b*) Umbelluzi, a locality practically at sea-level and devoid of evergreen forest, south-west of Lourenço Marquez. Yellow birds have also been collected here and greens would certainly not have been expected. The two greens (in the Smithsonian) were collected in July, and it has been suggested that they may be only winter-visitors to this untypical locality (Dr. Pinto, *in litt.*; Mr. D. W. Lamm, *in litt.*).

(*c*) Espungabera, *ca.* 2,800 ft. with evergreen forest patches, 400 miles to the north and only a few miles from Chirinda, over the border of Southern Rhodesia (see Map 8), has produced a typical yellow bird (wing 59, tail/wing ratio barely 70) and a typical green bird (wing 60, tail/wing ratio 75). As already noted, all the birds from the Rhodesian side of the border are all short-tailed and "yellow" except the one from Chimanimani that resembles the birds of the Nyasaland hill-forests. The Espungabera dark bird seems to be an isolated example of South African *virens*.

Thus, on the evidence from Zululand, the yellow and the green birds would certainly be regarded as specifically different. The Portuguese East African distribution is not so definitely in favour of this view, and moreover there are specimens whose plumage is intermediate. A male "yellow" from Umbelluzi (where, as noted, typical greens also occur) is darker and duller than the other Portuguese East African yellows; two females from Boane and Lourenço Marquez are darker above than the other yellows, and one of them also has as much melanin below as a green-belly. Interbreeding has, however, not been observed.

Taxonomic conclusions

These are reached with hesitation and must be regarded as provisional:

(*a*) Grey-bellies, *capensis* in the west intergrading with *atmorii* further east, are conspecific with green-bellies (*virens*).

(*b*) This group is specifically distinct from yellow-bellies (*anderssoni*).

(*c*) Pale-bellies (*pallida*) form a monotypic species. (There is no reason at all to connect them with other forms elsewhere in Africa that lack yellow on the belly.)

(*d*) Vaals ("*vaalensis*") are merely a colour-phase of *pallida*.

PART 5

INSULAR POPULATIONS

THE GULF OF GUINEA ISLANDS

The developments that have taken place in the Zosteropidae of the Gulf of Guinea are of special interest. Some of the birds concerned have so far differentiated that they have usually been regarded as worthy of separate specific and generic rank; and, unlike what happens on the African continent generally, apparently complete sympatry of two forms of Zosteropidae occurs in several cases. The situation is sketched diagrammatically in Text-fig. 11 with mean wing and tail measurements.

There are four islands, all of volcanic origin and lying on an axis S.S.W.–N.N.E. that extends to Cameroon Mt. on the mainland. Annobon appears to be drier than the other (very wet) islands, but all still carry a good deal of primary forest. Their age is uncertain, but they are believed to be post-Miocene, the result of the tectonic activity that has affected the whole of Africa since the end of the long early-Tertiary

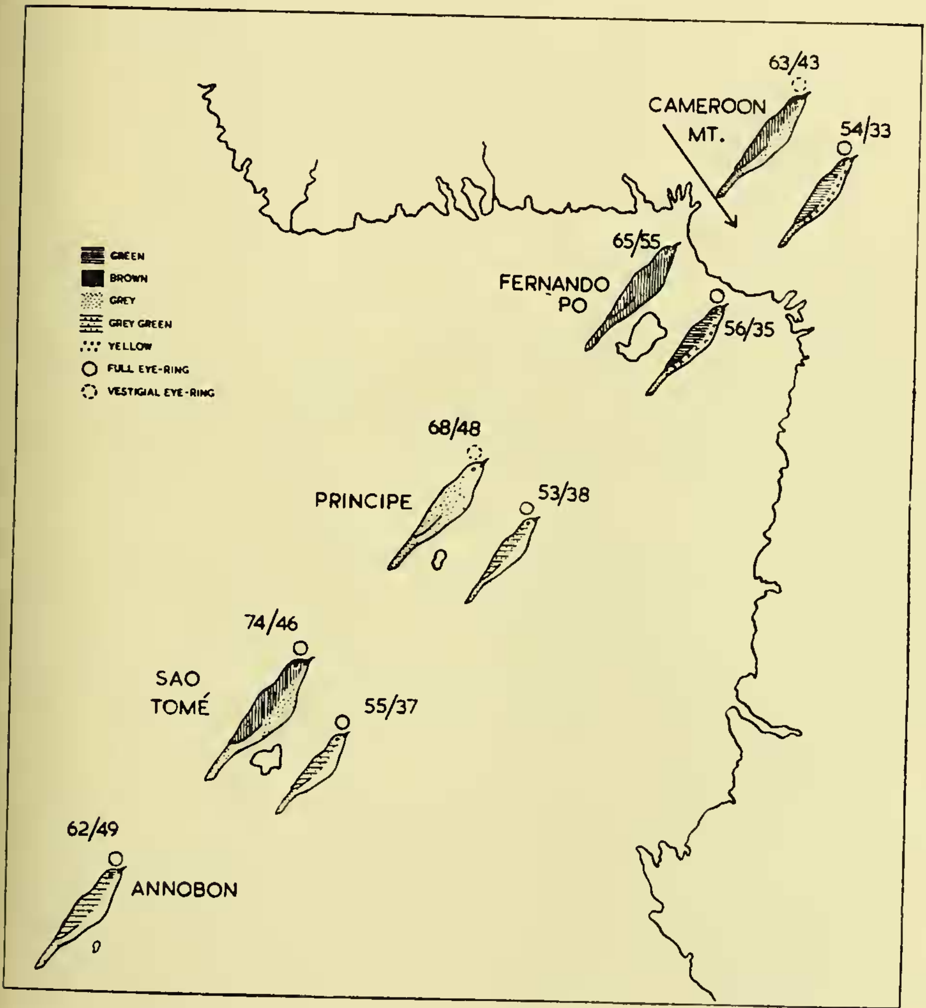


Fig. 11. The Zosteropidae of the Gulf of Guinea.

calm. Exell (1944) has given a useful general account of the islands and Snow (1950) of the central pair, São Tomé and Principe, with particular reference to bird-habitats. Amadon (1953) has recently published lists, with a comprehensive discussion, of the Gulf of Guinea avifauna, in which, however, he has kindly left the Zosteropidae to me.

The islands (Text-fig. 9) are, from north to south :

Fernando Po, about 800 sq. miles, only 20 miles off-shore and rising to 9,300 ft. —133 species of birds.

Principe, 50 sq. miles, about 130 miles from Fernando Po and also from the mainland, and rising to 3,100 ft.—30 species of birds.

São Tomé, 400 sq. miles, about 85 miles from Principe, 140 miles from the mainland, and rising to 6,600 ft.—47 species of birds.

Annobon, under 7 sq. miles, about 110 miles from São Tomé, 210 miles from the mainland, and rising to 2,000 ft.—9 species of birds.

The three southern islands are typically "oceanic" in the biological sense and each is surrounded by water 6,000 ft. deep. Fernando Po is "continental", with sea only 200 ft. deep separating it from the mainland. There, little more than twenty miles from Fernando Po, stands Cameroon Mt., an isolated volcano rising to 13,300 ft., with which Fernando Po has the closest biological affinities. Indeed, for the purposes of the present discussion, Cameroon Mt. must be regarded as a Gulf of Guinea island. (The only other typically montane forest avifaunas in the western half of Africa are those on the mountains immediately to the north-east, Kupe, Manenguba and the Banso-Bamenda highlands, with which that of Cameroon Mt. has much in common.)

The diversity of the avifauna on each island is no doubt partly a reflection of its size and variety of habitats, but also partly of its chances of receiving immigrants. Throughout the year the wind over this eastern part of the Gulf of Guinea is predominantly S.S.W. (Meteorological Office, *in litt.*), thus favouring movement neither southwards down the chain Fernando Po–Principe–São Tomé–Annobon, nor direct from the continent to any of the islands. On biological grounds, from a consideration of the insular avifaunas as a whole, Amadon (1953) has concluded that each of the three oceanic islands must to a large extent have received its birds independently from the mainland.

Annobon is inhabited by only one member of the Zosteropidae, but Fernando Po, Principe, São Tomé and Cameroon Mt. are each inhabited by two, one larger and with less yellow pigment than the other. Dimensions are given in Appendix 3 (Part 2) and other salient details are summarized in Table 3 (see also Note 27, Appendix 3). Even though they show no striking modifications in beaks, there is, of course, a presumption that such sympatric pairs of closely related birds differ in their feeding habits, if not in their habitats (*cf.* Lack, 1944 ; Moreau, 1948). The larger birds of each of these Gulf of Guinea pairs differ widely between themselves, but they are all so different from normal *Zosterops* that they have been kept together in the genus *Speirops* (see Note 28, Appendix 1). It may be added that at least three

TABLE 3.—*Colour Characters of Gulf of Guinea Birds.*

Form.	Colour of— Head.	Rest of upper parts.	Underparts.	Legs.[1]	Beak.[1]	Nature of eye-ring.
Aberrant:						
(1) Cameroon Mt. (*melanocephala*)	Blackish	Brown	Grey	Fleshy white or creamy white	Fleshy white or creamy white	Vestigial
(2) Fernando Po (*brunnea*)	Brown	,,	Brown	Dusky	Dark	Absent
(3) Principe (*leucophoea*)	Whitish	Grey	Pale grey	Pearl grey with yellow soles	Upper mandible dark grey, lower whitish	Vestigial
(4) São Tomé (*lugubris*)	Black	Olive-brown	Grey washed olive	Flesh	Yellow brown, upper mandible darker	Normal (medium)
Others:						
(5) Cameroon Mt. (*stenocricota*)	Yellow-green	As head	Yellow, flanks green	Grey	Black	Normal (medium)
(6) Fernando Po (*stenocricota*)	As (5)	,,	As (5)	,,	,,	,,
(7) Principe (*ficedulina*)	Olive-grey-green	,,	Whitish tinged sulphur	Pale brownish grey	Upper mandible dark horn, lower pale	,,
(8) São Tomé (*feae*)	Greyer than (7)	,,	Slightly greyer than (7)	Perhaps paler than (7)	Whitish tipped blackish	,,
(9) Annobon (*griseovirescens*)	Near (7)	,,	Near (7), fawn on flanks	Grey	Bluish horn	,,

[1] All except (1), (3), (4), (5) and (9) have, in the absence of collector's data, been based on colours of dried specimens.

of the *Speirops* and one of the insular *Zosterops* (São Tomé) differ from all the continental *Zosterops* examined by Dr. Auber in that melanization is not confined to the barbules but extends also to the barbs.

What little is known of the ecology of the nine birds may be outlined as follows :

(1) Cameroon Mt. at 6,000–9,000 ft. is inhabited by the brown endemic *Speirops melanocephala*, a bird which frequents the trees and shrubs in the montane grassland as well as clearings in the forest (Serle, 1950). Towards its lower limit this bird overlaps and associates with the smaller, yellow-green, *Zosterops stenocricota*, already discussed in Part 4.

(2) On Fernando Po, the common Zosteropid is the Cameroon *stenocricota* (see Note 27, Appendix 1) ; the other species, the endemic *brunnea*, is so rare that only two specimens exist in museums and nothing is known of its ecology.

(3) On Principe, the aberrant (grey) Zosteropid, *Speirops leucophoea*, is far bigger than its companion, the greenish *ficedulina*, but not bigger-beaked in the same proportion. No details are known of either bird, except that Snow (1950) found *leucophoea* in the lowlands, probably less abundant than it was first described to be in 1865, but yet more so than *ficedulina*, which he failed to see at all. (Correia collected some, however, in 1928—Amadon, 1953.)

(4) On São Tomé, the situation is like that on Principe. The aberrant bird, *Speirops lugubris*, is the largest of all the western Zosteropidae. Its disparity in wing-length with the *Zosterops* of the island, *feae*, is greater than that between any other of the pairs under discussion ; but, as in Principe, the two Zosteropids show rather less disparity in beak- than in wing-length. Snow (1950) found *lugubris* only from about 3,000 ft., above which it was common in the forest ; but he tells me that, unlike what obtains on Principe, such vegetation is lacking at the lower levels, so that *lugubris* may not be typically montane. Snow did not see *feae*, though Correia was able to collect a series in 1928 (Amadon, 1953).

(5) Annobon, so much smaller and less mountainous than the other islands, possesses only two passerines, a Paradise Flycatcher and the grey-green *Z. griseovirescens* (see Note 29, Appendix 1). It is the largest of the Gulf of Guinea *Zosterops*, smaller than the *Speirops*, but as big as most of the East African montane *Zosterops*. It was still plentiful throughout its wooded island when last reported in 1912 (by Boyd Alexander, in Bannerman, 1915).

When the foregoing information is considered together with the dimensions in Part 2 of Appendix 3, and the other characters outlined in Table 3, several points of interest emerge, which are discussed below.

Colour and pigments

All the insular Zosteropids have tended to lose yellow pigment with the exception of the Fernando Po *Zosterops*. This shows at most only incipient divergence from the nearby Cameroon *Zosterops*, presumably because of its recent arrival on the island or to frequent interchange of populations (or to a combination of these two factors).

As regards melanization, it is surprising that mainly (A)-type, i.e. black, pigment is present in the *Speirops*, which are predominantly brown or grey, and also in the São Tomé *Zosterops*, which is dull olive-grey-green. This colour is reproduced in the Principe *Zosterops*, which has not been examined microscopically, and also in the Annobon bird, but here its basis is (B) melanization (brown pigment). Since Annobon is much the driest island, the difference in pigment type is correlated with climate in the expected way. On the other hand, it is entirely unexpected that the colour (as distinct from the pigment) of the *Zosterops* should be so similar on both the wet islands and the dry, and also so like the colour of the dry-lowland *Zosterops* of Abyssinia. It appears that the pale colour of the São Tomé and Principe *Zosterops* cannot be a climatic adaptation.

Colour of beak and legs also tends to be abnormal in the Gulf of Guinea birds. On the African continent all beaks are black except some of the Abyssinian, which are brown. All the Gulf of Guinea birds depart from this in various ways. And in having their legs and feet whitish or flesh-coloured instead of more or less grey the Cameroon and São Tomé *Speirops* are distinguished from all the other Zosteropidae here reviewed.

The white eye-ring that occurs complete, though in a variety of sizes, in every *Zosterops* on the African continent, is vestigial in the black-headed *Speirops* of Cameroon Mt. and the white-headed *Speirops* of Principe and is completely absent in the brown *Speirops* of Fernando Po. Apparently the eye-ring is lost fairly easily in Zosteropidae, as has occurred in *uropygialis* of one of the Kei Islands, alone among the *chloris* group inhabiting that area (Stresemann, 1931). In the Gulf of Guinea the white eye-ring is being lost not only in a white-headed bird, in which contrast is in any case minimized, but also in a black-headed bird, in which contrast would be particularly strong.

Dimensions

In size—as judged by wing-length—the insular forms that are aberrant in plumage have also all become abnormally large. The Principe and São Tomé birds are both larger than any on the mainland of Africa. The only parallel is to be found in the most aberrant of the Pacific island birds, especially *Rukia*. Judging from the altitude/wing-length correlations on the continent (Text-fig. 1), the little-known Fernando Po bird is also abnormally large unless it is confined to the highest part of the 9,000-foot peak. Each of these aberrant birds presumably belongs to stock that has been longer on the island concerned than the less aberrant local *Zosterops*; and Amadon (1953) has already noted that the tendency of Gulf of Guinea insular birds to be big is especially marked in presumptive first-colonists such as these *Speirops* are.

From south to north the four *Speirops* form a series of diminishing size—São Tomé 74 mm., Principe 68, Fernando Po 65, Cameroon Mt. 63. No general reason can be suggested for this. As shown in Part 3, on the continent wing-length is closely correlated with both altitude and temperature. Lack of meteorological records and ignorance of the average altitude of the available specimens of each Gulf of Guinea form make it impossible to test the temperature correlation for these birds. It is, however, most unlikely that it would hold good, because the Cameroon *Speirops*, which is the smallest of the birds in question, comes from much the highest average altitude (8,000 ft.). The other stations are both more maritime and nearer the equator ; and there is no reason to suppose that the insular Zosteropids in question experience lower temperatures than the high-altitude birds of Cameroon Mt. I conclude that the large sizes attained by the *Speirops* are due to local biological causes and that there is no general reason for their arrangement in a series of decreasing wing-length northwards.

In contrast to the *Speirops*, except on Annobon none of the *Zosterops* diverges obviously in size from expectation (though again the data do not suffice for correlating wing-length with temperature). On Annobon, which does not rise above 2,000 ft., and which contains only one passerine besides the *Zosterops*, the latter is larger than expected. But on each "island" possessing two Zosteropids the less aberrant bird is the smaller, to a very variable degree. The difference in mean wing-length between *Speirops* and *Zosterops* is 19 mm. on São Tomé, 16 on Principe and only 9 mm. on Cameroon Mt. and Fernando Po.

Tail/wing ratios vary remarkably. At one extreme the Fernando Po *Speirops* appears to have a longer tail in proportion to wing (ratio over 82) than any other population of the western Zosteropidae (though individual South African birds exceed 80). At the other extreme the São Tomé *Speirops* has an abnormally short tail (ratio 61·8), equalled in this respect only by the *Zosterops* of the opposite mainland (as exemplified by those of Cameroon, with ratio 61·6). The insular *Zosterops* show a similar lack of uniformity. The Fernando Po bird is, like the Cameroon, abnormally short-tailed (62·8) by continental standards. The Principe and São Tomé birds have much higher, more "normal", ratios, 71·7 and 67·2 respectively, while the Annobon bird with ratio 77·6 is at the top end of the continental range. Thus there is no reason to regard the short tail of the São Tomé *Speirops* as evidence of particularly close affinity with the short-tailed but otherwise normal *Zosterops* of the neighbouring mainland. In fact, as discussed in Part 3, tail/wing ratio is of uncertain taxonomic significance.

The beak/wing ratio varies in the nine forms under discussion between 21% and 26%. The insular *Zosterops* have longer beaks in proportion to their wings than the insular *Speirops* (this does not apply to the Cameroon Mt. populations). In fact, against a mean beak/wing ratio of 22·7 for the continent of Africa as a whole, the mean beak/wing ratio of the *Speirops* in the Gulf of Guinea islands is only 21·3, while that of *Zosterops* is 24·5. Thus the *Zosterops*, but not the *Speirops*, accord with Amadon's (1953) generalization (based on other species) that insular birds tend to have larger beaks than their nearest relatives on the mainland. This might suggest that the *Speirops*, in the course of their evolution to their present stage of abnormality, passed through a phase in which their beak/wing ratio rose above that of the continental birds but that later, with increasing body-size, the process was reversed. On this hypothesis the Annobon bird is in the intermediate stage, with beak/wing ratio still high but body-size becoming abnormally large.

General

The Zosteropids of the Gulf of Guinea must have been derived originally from the opposite mainland, in at least some of the islands by two distinct colonizations. But which of the existing forms were evolved *in situ* from colonists direct from the mainland and which were derived from inter-island invasion cannot be determined. Any discussion could be little more than speculative, especially as the characters of the ancestral mainland *Zosterops* can only be surmised.

A main general change in all the insular birds is the loss of yellow pigment ; and it is difficult to suggest why this should be so, especially since, as has been shown, plumage colour is not correlated with climate.

The several *Speirops* differ from each other and from "normal" *Zosterops* in so many characters and to such varying degrees that it is impossible to decide which is the most primitive or the most "specialized". Those of Cameroon Mt. and São Tomé are sufficiently alike to be regarded as conspecific, and this although two islands, each with a very different *Speirops*, intervene geographically. The São Tomé bird has not lost eye-ring and yellow pigment to the same extent as the Cameroon bird, which suggests that the former is the nearer to the ancestral stock, and hence that the Cameroon bird is an invader from an island. On the other hand, the whitish on the forehead and throat of the Cameroon bird, which is lacking in the São Tomé, is adumbrated in those numerous "normal" *Zosterops* which have yellow on the forehead and throat contrasting with a generally green head. Hence in head-pattern the Cameroon bird may be regarded as retaining primitive characters that the São Tomé bird has lost. In any case it seems best to recognize the closeness of resemblance between the Cameroon and the São Tomé *Speirops* by treating them as conspecific. The Principe *Speirops*, with its very pallid foreparts, and the Fernando Po bird have evolved on different lines from the other two.

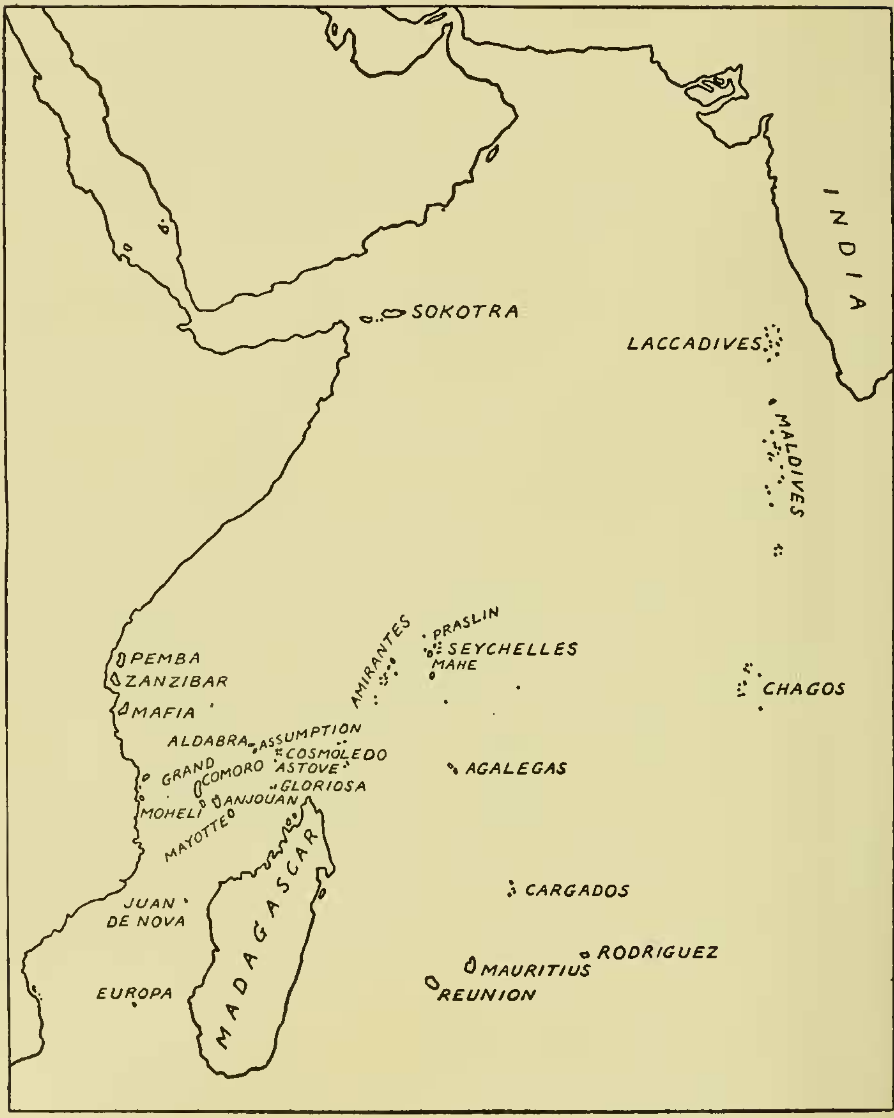
The *Zosterops* of Principe and São Tomé are so alike that one is more likely to have been derived from the other rather than both evolved, convergently, from independent colonists from the mainland. In general colour the Annobon *Zosterops* is so like these two that it has sometimes been regarded as conspecific ; but it is sufficiently different in size and proportions for this to seem undesirable.

Hence we get the following classification : *Zosterops senegalensis stenocricota* on Fernando Po, *Z. ficedulina ficedulina* on Principe, *Z. ficedulina feae* on São Tomé, *Z. griseovirescens* on Annobon. *Speirops lugubris melanocephala* on Cameroon Mt., *S. lugubris lugubris* on São Tomé, *S. brunnea* on Fernando Po and *S. leucophoea* on Principe.

THE ISLANDS OF THE INDIAN OCEAN

Zosterops are widely distributed in the Indian Ocean and belong to at least six species. Most of the islands fall into two groups (see Map 12), those inhabited by *Zosterops* being denoted in the following paragraphs by an asterisk.

(*a*) Low limestone islands, mostly atolls, of which there are a great many, especially in the east, where the Laccadive*, Maldive and Chagos archipelagos are separated



Map 12. The Indian Ocean.

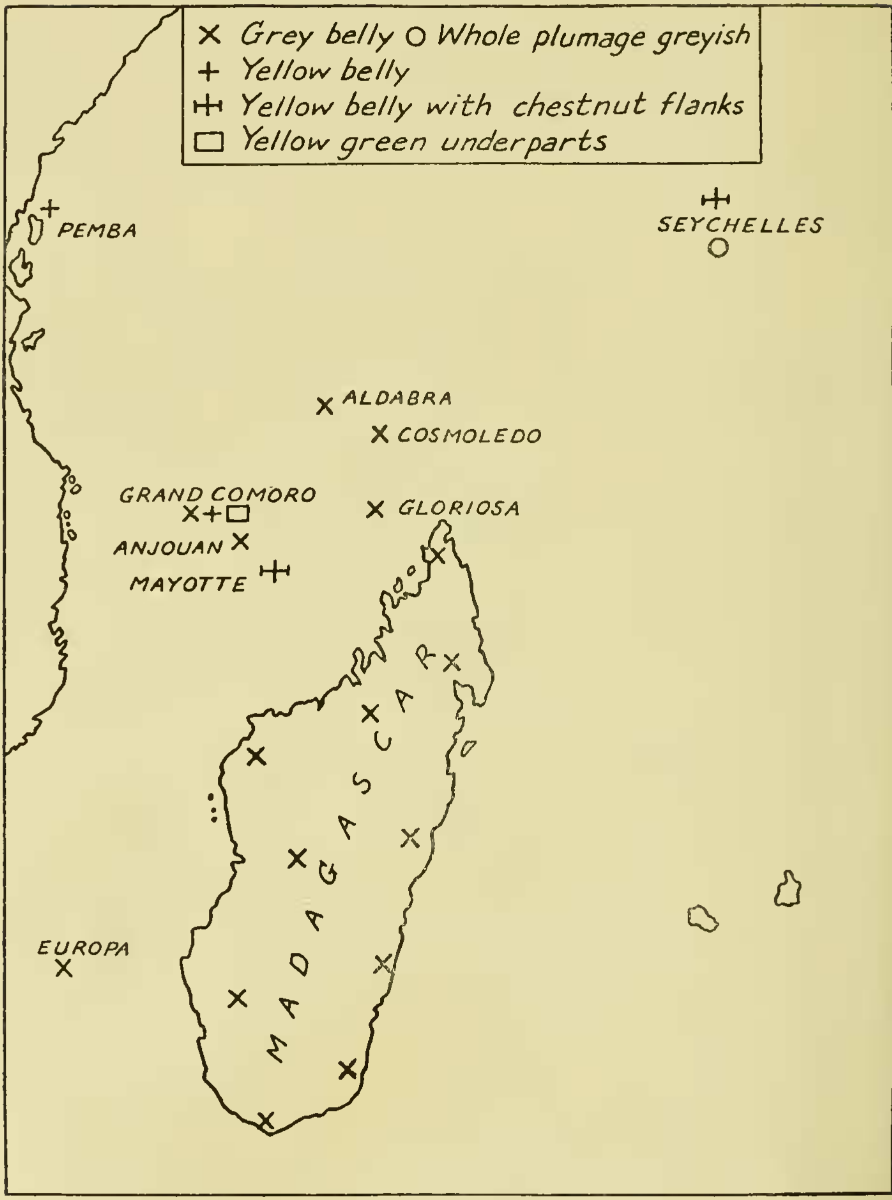
by 1,200 miles of uninterrupted sea from the Mascarenes. Other coral islands form the Cargados, the Amirantes, other outliers of the Seychelles and, nearer Madagascar, the Aldabra group*, Gloriosa*, and, in the Mozambique Channel, Juan de Nova (17° 4′ S., 47° 43′ E.) and Europa Island* 22° 20′ S., 40° 20′ E.). None of this class of island has an area of more than a very few square miles and most of them are only a few hundred acres. The natural vegetation appears to have been scrub jungle and much of it has been replaced by coconuts.

TABLE 4.—*Main Colour Characters of Indian Ocean* Zosterops.

N.B.—All have a small eye-ring.

Islands.	Upper parts.	Yellow on head.	Underparts.
Madagascar group :			
(1) Madagascar[1] *maderaspatana*	Yellow-green[1]	None.	Whitish more or less washed brownish grey
(2) Gloriosa	As the yellowest of (1)	,,	As (1)
(3) Cosmoledo	? Paler and less yellow than (1)	,,	,,
(4) Europa	As (1)	,,	,,
(5) Aldabra *aldabrensis*	Yellower than (2)	Variable on lores and forehead	,,
(6) Laccadives	Yellower than any above	As (5)	As (1) but clearer
Comoros :			
(8) Grand Comoro *comorensis*	As (2)	On lores and forehead	As (1)
(7) Anjouan *anjouanensis*	Slightly yellower than (1)	On lores	,,
(9) Grand Comoro *kirki*	Yellow green	On lores and forehead	Golden-yellow, green on flanks
(10) Grand Comoro *mouroniensis*	Greener than (9)	On lores	Greenish yellow
(11) Mayotte *mayottensis*	Greenish-yellow	On lores and forehead	Golden yellow, reddish at sides
Seychelles :			
(12) Marianne *semiflava*	Slightly yellower than (11)	Less than (11)	Brighter than (11)
(13) Mahé *modesta*	Grey-brown tinged olive	None	Pale grey-brown
Mascarenes :			
See Table 5			

[1] Marked local variation, the birds being darkest in the wettest areas, yellowest in the driest.



MAP 13. The distribution of *Zosterops* colour in the Indian Ocean islands.

(*b*) Other "oceanic" islands, the Comoros*, Mauritius*, Reunion*, Rodriguez and the Seychelles*; most of these are mountainous and all are volcanic except the last. They range in size from the single square mile of (granitic) Marianne in the Seychelles to the 270 square miles of Mauritius. All seem to have been covered with forest when discovered about 400 years ago, the smallest of the Seychelles being the driest. The Seychelles group, the Comoros group and each of the other islands are surrounded by deep water. Nothing certain is known of their age, but in view of the general tectonic tranquillity during the earlier half of the Tertiary there is little doubt that the volcanic islands are post-Miocene; the Seychelles may well be much older.

Apart from these two classes of typically oceanic islands there are in our area :

(1) the great island of Madagascar*, which is in a class by itself ;

(2) numerous islets which are no more than the tips of coastal reefs surrounding Madagascar or the African continent ;

(3) the two big inshore islands of Zanzibar and Mafia (640 and 240 square miles), typically "continental" both biologically and geographically ;

(4) Pemba Island* (380 square miles), less than thirty miles from the African mainland but not typically continental.

(5) Sokotra* (and neighbouring islands) off the "Horn of Africa" (Somaliland). Its *Zosterops*, which is like the Somali bird, has already been dealt with in the section "North-east Africa".

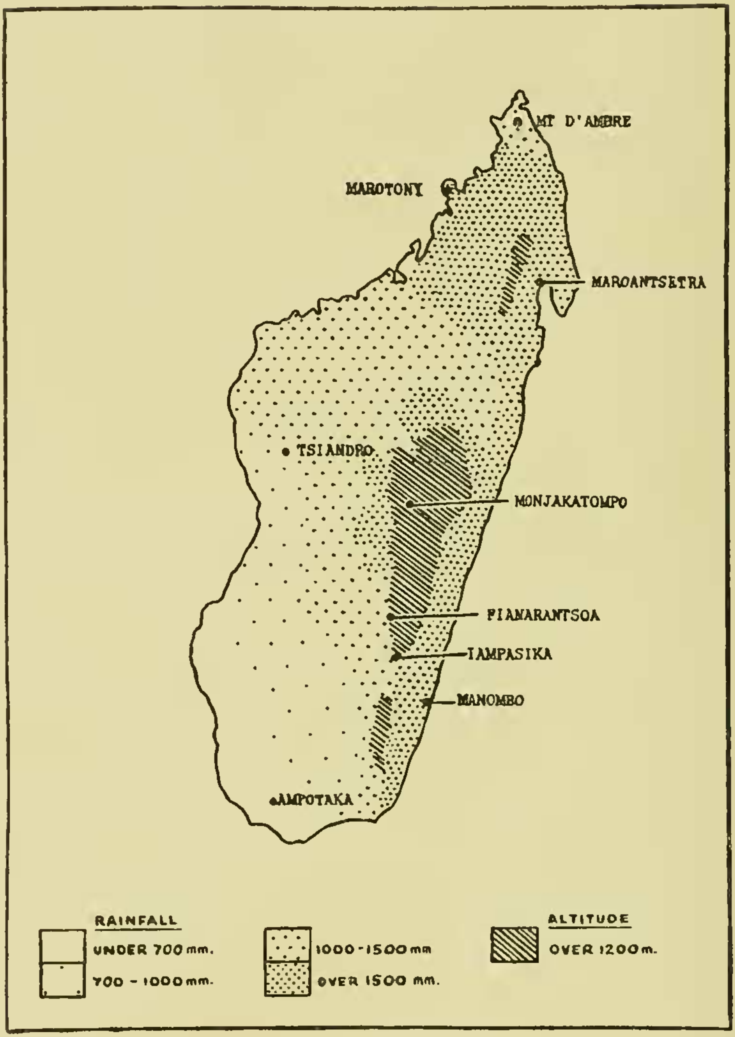
The main colour-characters of the Indian Ocean *Zosterops* are outlined in Table 4 (dimensions in Appendix 3, Part 3) and the distribution of these is given in Map 13). The island populations will now be dealt with separately.

Pemba Island

Pemba is geologically and biologically peculiar (Moreau and Pakenham, 1941). Though only thirty miles from the African coast it is separated by water 2,000 ft. deep and has a *Zosterops* as one of its commonest birds (Vaughan, 1930) ; whereas the neighbouring islands of Zanzibar and Mafia, which are on the continental shelf, lack *Zosterops* though apparently suitable for them. The Pemba bird, *vaughani*, is small and richly coloured, with an unusually bright golden-yellow forehead. In this respect (though no other) it approaches the montane *Zosterops* of eastern Kenya, but it is separated geographically from these by other *Zosterops* that are very different. There is also no reason to suppose that the *Zosterops* now occupying the nearby East African lowlands (*flavilateralis*), which looks very different from the Pemba bird, was its ancestor or is particularly closely allied ; and there seems no alternative but to treat the Pemba bird as a monotypic species.

Madagascar

As shown in Map 14, the driest parts of Madagascar (200,000 sq. miles) are the extreme northern tip, with rainfall under 40 inches, and the south-west, with under 30 and a strongly xerophytic vegetation. The whole of the east coast, except the far north, is wet (rainfall 60–140 inches) with much of the natural vegetation evergreen



MAP 14. Madagascar.

forest; and rainfall of over 60 inches extends across to the north-west coast. Most of Madagascar is lowland, but the land rises to 8,600 ft. in the east centre, and further to the north and south there are small detached areas above 4,000 ft.

Because so much of the Madagascar fauna is highly peculiar it is surprising that the single species of *Zosterops* occurring there should be "normal" and unspecialized. With its green upper parts and whitish underparts more or less clouded with grey the Madagascar *Zosterops* resemble many others, notably those of Abyssinia. In different parts of the island they vary in size and in the amount of melanin. The darkest birds are found in the area of highest rainfall in the east; those with yellowest backs (least melanin) come from the extreme south-west, and the next yellowest from Mt. d'Ambre, in the dry area at the opposite end of the island. Intervening birds (for example, a series from Tsiandro) are intermediate in colour, while birds from the north-west, round Marotony, cannot be distinguished from those with the same rainfall, about 1,500 mm., in the south-east (Manombo). As regards the underparts (in which the individual variation is great), birds from the wettest area in the island, Maroantsetra on the north-east coast, have on the whole the most (and more brownish) grey shading than any others, and those of the dry south-west have the least.

Size also varies as expected, in that birds from the highest locality (in the east centre) are the biggest. However, the smallest are from two detached areas, the very wet Maroantsetra on the north-east coast, and the south, including both Ampotaka, which is very dry, and Manombo, which is rather wet. Comformably, the south-western birds have slightly the smallest beaks, as Salomonsen (1934*b*) has claimed.

Salomonsen (1934a, 1934b) described the yellowest, "dry", birds as *ampotakae* and the biggest birds as *analoga*, confining *maderaspatana* to the humid east at low altitudes and considering that many birds in the island are intermediate between *ampotakae* and *maderaspatana*. Rand (1936), on the other hand, while recognizing that the birds from the south-west and from the extreme north are both yellower than those in between, is content to call all the western birds *ampotakae*—with the extraordinarily wide habitat-range of "humid forest, dry forest, secondary brush and subdesert brush". As regards the large "subspecies" *analoga*, there is no doubt that the virtual discontinuity claimed between its size-range and that of *maderaspatana* is due to paucity of samples from intermediate altitudes (see Note 30, Appendix 1). In fact the true picture of the Madagascar *Zosterops* is of a series of trends in size and intensity of melanin that are in conformity with the changing environment. The use of three trinomials tends to obscure the biological facts. (For the individuals lacking carotenoid, on which *Z. hovarum* and *Z. praetermissa* were described, see Note 2, Appendix 1.)

The Comoro Islands

The Comoro group consists of four volcanic islands (with very few off-lying islets), the most westerly, Grand Comoro, being 180 miles from the African mainland and the most easterly, Mayotte, 190 miles from Madagascar. Each island is in sight of one or two others, 30–60 miles distant. Approximate sizes and altitudes are ;—

Grand Comoro, 420 sq. miles, 8,000 ft.; Mohéli (Mohilla), 150 sq. miles, 2,400 ft.; Anjouan (Johanna), 140 sq. miles, 4,900 ft.; Mayotte, 140 sq. miles, 2,000 ft.

Apparently a larger proportion of the original forest is left on them than on the other islands in the Indian Ocean (Grandidier, 1934). Individual islands have from one to three different *Zosterops* on them, as follows:

(1) The Mayotte *Zosterops* is short-tailed (ratio 63) and bright yellow with chestnut on the flanks (sometimes extending across the breast). It is unlike every other *Zosterops* except *semiflava* of the Seychelles, 800 miles away to the north-east, and particularly unlike the neighbouring Madagascar birds. Nothing is known of its ecology except that Nicoll (1908) found it one of the commonest birds of the island, "especially on the edges of the mangrove swamps".

(2) Anjouan birds differ from those of Madagascar only in being a little yellower, with a tendency for the yellow on the throat to extend a little further down the breast. Anjouan beaks are also perhaps a trifle stouter than those on Madagascar or Aldabra (Friedmann, *in litt.*, agrees), but in other dimensions there is little difference from Madagascar birds. Nothing has been recorded of the Anjouan *Zosterops* in life. It is apparently confined to that island, the record of *anjuanensis* for Grand Comoro in Shelley (1879) and Milne-Edwards and Oustalet (1888) really relating to *comorensis* (see below).

(3) On Mohéli Völtzkow (1917) recorded *kirki*, one of the Grand Comoro birds (see below). This may or may not be correct. No museum seems to possess a Mohéli *Zosterops* and Professor Stresemann (*in litt.*) thinks Völtzkow's record is on sight—useless in such a case.

(4) Grand Comoro, the biggest and loftiest of the four islands, seems to have three *Zosterops*. Nothing is known of any of them in life.

(*a*) *Z. comorensis*, a bird with a whitish belly (see Note 31, Appendix 1) was described by Shelley from a single specimen, in poor condition and not sexed, which is still the only one known. It differs from the Madagascar and the Anjouan birds only in having a little more yellow on the front of the head and being a little smaller. In conjunction, these slight differences suggest that the specimen does represent an indigenous Grand Comoro population rather than being merely wrongly labelled or a straggler from Anjouan, sixty miles to the east. Only field-work can settle this.

(*b*) *Z. kirki* is a richly coloured yellow-bellied bird with a range of wing-length and tail-length that includes the dimensions of the only specimen of *comorensis*. Moreover the tail/wing ratio is the same and the beak practically so. The possibility that this and *comorensis* are merely colour-phases cannot be ruled out.

(*c*) The third *Zosterops* described from Grand Comoro, *mouroniensis* (see Note 32, Appendix 1), is quite distinct from any other of the Indian Ocean birds; it is large and dark, and the only one to have yellow underparts heavily flushed with green. Its wing averages 62 compared with 53 in the other *Zosterops* on the island, and its tail/wing index is the abnormally high one of 79, which compares with 67. The beak of *mouroniensis* is not, however, proportionately longer and stronger than it is in the smaller birds. This is correctly suggested in plate 5 of Milne-Edwards and Oustalet (1888), though the plumage is probably there depicted too yellow. The large size and dark plumage of *mouroniensis* are exactly what would be expected in a highland bird, but it is not known to be so, although the island contains a 9,000-foot mountain.

The Seychelles

This mountainous group is more isolated than the Comoros, being 900 miles from the African mainland (with no islands on the way), 600 from Madagascar (with atolls at intervals) and about 500 from Aldabra, the nearest *Zosterops* population. E. Newton (1867) found that at least five of the islands supported from two to five species of native passerines and Vesey-Fitzgerald (1940), while chronicling some disappearances, was able to record also some additions. It is therefore remarkable that the only certain evidence of Zosteropidae in the Seychelles is of one form (*modesta*) on Mahé (55 sq. miles, the biggest of the group) and one (*semiflava*) that formerly inhabited tiny Marianne Island, less than one square mile (see Note 33, Appendix 1).

In size, proportions, eye-ring and beak, both *modesta* and *semiflava* are typical *Zosterops* and are very much alike ; but their colourings are as different as possible (see plate 6 in Shelley 1900, vol. 2). *Z. modesta* is a muddy-brownish bird almost entirely devoid of yellow pigment. Vesey-Fitzgerald (1940) has already noted that most of the Seychelles passerines have tended towards the same dingy olive plumage, as elsewhere in small isolated avifaunas. By contrast, *Z. semiflava* has bright olive-yellow upper parts and golden yellow under-parts with bright chestnut sides. Thus *semiflava* is unlike any other *Zosterops* except the Mayotte bird 800 miles away to the south-west (and with the very different Madagascar type of *Zosterops* on intervening atolls). Indeed *mayottensis* differs from *semiflava* only in being smaller and slightly yellower.

From its loss of yellow it is probable that *modesta* is a descendant of a much earlier invader of the islands than *semiflava* is. Since these two are so alike in size and beaks (and probably in habits) it is unlikely that they could co-exist for long on such small individual islands and they may at one time have divided the archipelago between them.

The Mascarene Islands — Réunion (Bourbon) and Mauritius

Réunion lies nearly 500 miles east of Madagascar and Mauritius 120 miles further east, but under 600 miles from the nearest point of Madagascar. Each is a volcano, probably not older than the Pliocene (Réunion is not extinct) and is surrounded by very deep water. Mauritius, with an area of 720 square miles, rises to 2,600 ft., Réunion, about 1,000 square miles, to over 10,000 ft. Since there is no land to the east bigger than Rodriguez (42 sq. miles) for 2,000 miles, the chances that Mauritius and Réunion received their birds from Madagascar are overwhelming, but the present wind-system does not favour dispersal in this direction. All through the year easterly winds predominate on the east side of Madagascar and in Réunion (Grandidier, 1934). Moreover the tracks of the local cyclones, potentially even more important agents of dispersal, are nearly all unhelpful. Of 74 cyclones plotted in this area (west of 70° E.) 1927–1937, only two passed over the east coast of Madagascar and then within 100 miles of either Mauritius or Réunion (Huddart, 1948).

Considering their isolation, the parallelism between the avifaunas of the two islands is remarkable. Nearly all the passerine species are common to both islands, and in the Zosteropidae each island possesses a long-beaked one that has lost some of its yellow pigment, and a short-beaked one that has lost all its yellow and its white eye-ring as well (see Note 34, Appendix 1). The plumage features of all four birds are summarized in Table 5, dimensions in Appendix 3 (Part 3).

TABLE 5.—*Colour Characters of Réunion and Mauritius Zosteropidae.*

	Head.	White eye-ring.	Upper tail-coverts.	Colour of rest of upper parts.	Under parts
borbonica (Réunion)	Brown	Absent	White	Brown	Whitish with cinnamon flanks
mauritiana (Mauritius)	Grey	,,	,,	Grey	Whitish with grey-brown flanks
haesitata (Réunion)	Blackish	Marked	Yellow-green	Yellow-green	Grey, more rufous on flanks; under-tail coverts greenish yellow
curvirostris (Mauritius)	Dark grey	,,	,,	Grey, becoming green on lower back	As *haesitata*

Briefly, *borbonica* on Réunion is a small brownish bird of normal proportions (wing 55, tail/wing ratio 73) with a beak (*ca.* 13·5 mm.) if anything weaker and more pointed than in typical *Zosterops*. Individual variation in adult plumage is exceptionally high (grey to brown), while the immature plumage is more uniformly brown (Berlioz, 1946). The Mauritian representative of *borbonica*, *mauritiana*, also completely devoid of yellow pigment, is usually grey, sometimes brownish. The greyest birds from Réunion are little browner than the brownest from Mauritius; and the two populations are alike in dimensions and in having white rumps. This last feature is presumably merely a derivative of the pale colour (yellow) on the rump which occurs in many *Zosterops* in Africa and elsewhere. There is no strong case for retaining these Mauritius and Réunion birds in a separate genus, *Malacirops*, nor for treating them as two separate species, as has been done in the past.

In both of the other pair of birds, *haesitata* of Réunion and *curvirostris* of Mauritius, the beak/wing ratios are higher than in any other western Zosteropidae and are exceeded only in a few forms on small islands in the Pacific. In both, yellow pigment has gone from the head, but the Réunion bird is more melanic than the Mauritian and also larger (wing 57·7 compared with under 52) and longer-tailed (ratio 70 against 63).

The present status of the Réunion birds has been described by Milon (1951). He found the smaller-beaked *borbonica* "très commun partout", with occupied nests from sea-level up as far as he went (1,300 m.). The longer-beaked *curvirostris* was "assez commun en fôret" from 500 m. upwards. This species is, then, more of a forest (and mountain) bird than the other. This is the reverse of what Pollen and Dam (1868) recorded over eighty years ago, but agrees with the distribution of the two related birds on Mauritius (see next paragraph). Milon also records that in the mountains they regularly inhabit the same biotope, trees and bushes. Their overlap leads him to postulate a difference in feeding habits (as the difference in beaks also strongly suggests), but he was unable to prove it. It is interesting that in Réunion *curvirostris* is regarded as having suffered much more severely than *borbonica* from the 1948 cyclone, a difference that might be connected with a tendency for the latter to roost nearer the ground (Milon, 1951).

On Mauritius the grey *mauritiana* has survived more generally and in larger numbers than the longer-beaked *curvirostris*, which is, as Meinertzhagen (1912) found, mostly in the remote forests of the south-western plateau and not numerous there (Dr. R. Vinson, *in litt.*, 1951). Apparently the two Mauritius species do not associate together (*ibid.*). *Z. curvirostris* is supposed to have suffered through destruction of its nest by the bulbul *Otocompsa jocosa*, which was introduced into Mauritius a hundred years ago, but not into Réunion (Berlioz, 1946). In Mauritius, as in Réunion, there are no observations on the food-habits of the two *Zosterops* which suggest specialization, though the difference in beaks suggests it.

The two birds devoid of yellow pigment, *borbonica* and *mauritiana*, differ only in that the Réunion bird is browner and has a beak a little narrower at the base than the Mauritius bird. By contrast, in the other, long-beaked, pair of birds, those of Mauritius are much smaller and shorter-tailed. Yet the beaks are nearly the same size, so that the beak/wing ratio in Mauritius is nearly 32 against 27 in Réunion. In Réunion the long-beaked *Zosterops* is a bigger bird than the short-beaked, but in Mauritius this is reversed. Yet the difference in each island between the beak-lengths of the two Zosteropids is the same, about 2 mm.

It is by no means clear whether *borbonica* and *mauritiana* or *haesitata* and *curvirostris* represent the earlier invasion into the Mascarene islands. The first pair have lost their eye-ring and all their yellow pigment and have acquired the unique feature of white upper tail-coverts. The second pair have lost the carotenoid from their throats, but not from all their upper parts, and they have considerably modified beaks. The beaks are in fact rather like those of *Zosterops zeylanica* (Ceylon), in which this change has taken place before pigment has been lost in the plumage. It seems that the present situation in the Mascarenes—both species present on both Réunion and Mauritius—could have arisen in two ways. Either *Zosterops* from Madagascar colonized Réunion or Mauritius; later, when the first colonists had already diverged considerably from "normal" *Zosterops*, a second invasion succeeded in establishing itself on the same island and also proceeded to diverge from the normal; then both at some later stage colonized the other island. Alternatively, and perhaps more likely, opportunities being what they were, Madagascar *Zosterops* colonized Mauritius and Réunion independently, the stock on each diverged from the "normal" and subsequently, when the evolution had gone far enough, each succeeded in establishing itself on the other's island.

Whichever of these hypotheses is correct, the fact that the Zosteropids, and most other passerines, on Mauritius differ at most subspecifically from those on Réunion, makes it most probable that interchange between them has not been infrequent ; the winds, as already noted, strongly favour movement from the outer island, Mauritius to Réunion, but not the other way.

The remaining islands

All the remaining insular populations are of Madagascar type, with whitish belly, and they occur on islets north and west of Madagascar except for those on the Laccadives, which are on the opposite side of the ocean, close to the Indian coast.

(1) On Aldabra, a dissected atoll about fifty miles round, the *Zosterops* is a little yellower, smaller and longer-tailed than Madagascar birds.

(2) On Gloriosa, less than two square miles, about 115 miles from the north end of Madagascar, the *Zosterops* are not distinguishable (see Note 35, Appendix 1). Nicoll (1906) found it "the most abundant land-bird" but there cannot have been more than a few hundreds.

(3) On Cosmoledo and Astove, fragmentary atolls between Aldabra, Gloriosa and Madagascar, *Zosterops* are common (Vesey-Fitzgerald, 1940) but material is insufficient to show whether the birds are distinctive (see Note 35, Appendix 1).

(4) On Europa, in the Mozambique Channel, sixteen square miles, about 250 miles from both Africa and Madagascar, the *Zosterops* differs from Madagascar birds only in having a higher tail/wing ratio (see Note 36, Appendix 1).

(5) The Laccadive *Zosterops*, while of the same colour-pattern as the preceding, is undoubtedly derived from the neighbouring Indian mainland. Ticehurst (1927) and Stresemann (1931) attributed them to the Ceylon subspecies *egregia* which would imply either invasion of the Laccadives from Ceylon round the tip of the Indian peninsula or convergent evolution. However, *egregia* is very like *occidentis* of western India and on comparing series I find that the Laccadives birds are actually intermediate in plumage.

General discussion

Considering the bigger sea-distances, the Indian Ocean Zosteropidae show less marked peculiarities then might have been expected from the situation in the Gulf of Guinea. The Indian Ocean birds as a whole tend to be slightly longer-beaked (mean ratio over 24) than would be expected by continental standards, but there is no gigantism, and where yellow pigment is lost the result is not the same dingy pallor of plumage as in the Gulf of Guinea *Zosterops*. On the Indian Ocean atolls the *Zosterops* have differentiated particularly little, even though the populations are so small, and they must all be regarded as correspondingly recent invaders.

It is remarkable that the *Zosterops* of Madagascar, an island possessing so many outstanding endemics, should not be in the least specialized. On the contrary they are so like both the Indian birds (*palpebrosa*) and certain African birds that convenience is the main reason for keeping them as distinct species.[1] It is possible that *Zosterops* of modern type were already in occupation of Madagascar before it was isolated from Africa. The generally accepted view is that this took place late in the Miocene (some twenty million years ago), when many of the present African genera may already have been in existence (see discussion in Moreau, 1952). It is true that the African *Zosterops* most like those of Madagascar do not occur on the continent just opposite the island, but the present *Zosterops* picture on the mainland is perhaps very recent on the evolutionary time-scale.

The Madagascar *Zosterops* may have remained "normal", partly because the area is so large and the fauna so rich—not typically insular—and partly because the original stock, if merely cut off from the continent, not invading, would have had so large an assortment of genes that there was no intrinsic tendency to unbalanced differentiation in the isolated environment (*cf.* Mayr, 1954). In any case, unless the Madagascar stock that gave rise to the *Zosterops* of Réunion and Mauritius has been superseded by the existing one, this has remained stable while two eccentric developments have taken place in the smaller islands.

The *Zosterops* of Aldabra, Anjouan, Gloriosa, Europa and Cosmoledo, as well as *comorensis*, resemble those of Madagascar so closely that they are probably all (down-wind) colonists from there. If their appearance is a guide, the other two *Zosterops* of Grand Comoro are successive invaders from Africa. This would be in line with the conclusion, reached by Milne-Edwards and Oustalet (1888), that the (highly endemic) Comoro avifauna as a whole has been derived from both Africa and Madagascar. If indeed two *Zosterops* so alike as *kirki* and *comorensis* co-exist on Grand Comoro it can only be through genetical incompatibility, and that would be more likely if the birds were derived from western and eastern stocks respectively.

Nothing can be hazarded about the origin of the Mayotte and Seychelles *Zosterops*, which are all three peculiar. But, because they share the very rare colour-combination of bright yellow and reddish, *mayottensis* and *semiflava* must have had a recent common ancestor, even though other, Madagascar, types of *Zosterops* intervene geographically. The wide geographical separation of these subspecies and of those of the Réunion and Mauritius *Zosterops* finds a counterpart in Micronesia, where subspecies of *Z. conspicillata* and *Z. cinerea* are dispersed over much greater marine distances in the Caroline and Palau islands (Baker 1951).

The following taxonomic arrangement seems justifiable :

Z. maderaspatana maderaspatana (Madagascar, Gloriosa and perhaps Cosmoledo), *Z. m. aldabrensis*, *Z. m. völtzkowi*, *Z. m. comorensis* ; *Z. senegalensis kirki* ; *Z. mouroniensis* ; *Z. semiflava semiflava*, *Z. s. mayottensis* ; *Z. modesta* ; *Z. borbonica borbonica*, *Z. b. mauritiana* ; *Z. curvirostris curvirostris*, *Z. c. haesitata*.

[1] For example, some birds from Madagascar match birds from Abyssinia (*poliogastra*) except in lacking yellow on the forehead and having the throat a stronger, less greenish, yellow. Again, Madagascar birds differ from the grey-bellied birds of the Cape only in the shade of green on the upper parts, purer yellow of the throat, and paler underparts, especially in the centre.

PART 6

SYNTHESIS

Throughout this study the overwhelming general impression has been the close correlation of the *Zosterops* dimensions with altitude and temperature, and also the correlation, though less constant, between colour of plumage and type of climate. These correlations on the one hand ensure high local variation, largely clinal, and on the other hand favour convergent evolution. The first of these results means that, if trinomial nomenclature is applied, the variation admitted within the subspecies must, for practical purposes, be wide and the delimitation of their range cannot be precise. The second result means that, following current ornithological usage, on purely morphological criteria the same subspecific name will on occasion be used for geographically remote populations that are convergent products of independent local evolution. So far as the problem of the specific limits of the African *Zosterops* is concerned the obvious guiding principle is that forms which intergrade geographically and in characters must be treated as members of the same species (*cf.* Cain, 1954) ; special difficulties arise where there are discontinuities, as between islands.

It will have been evident, particularly from the discussion on the significance of belly colour (Part 2), that attempts to use the colour aspect of "morphological" difference consistently as a specific criterion in *Zosterops* must break down. We are repeatedly thrown back on the criterion of occurrence of interbreeding, one particularly unsatisfactory in these *Zosterops*, where hybrids are likely to be difficult or impossible to diagnose with certainty and series of critically collected material are not as a rule available. As mentioned in the introduction, interbreeding between two "morphologically" different forms of *Zosterops* that are neighbours in Africa rarely seems quite impossible on grounds of "genetical allopatry" ; and a few specimens have been mentioned in the text that look as if they were hybrids. If such hybrids form only a small proportion of the total *Zosterops* population where two forms meet, or the zone in which hybrids occur is narrow, and/or the hybridization is of the "secondary" type, with high variation between the hybrid individuals, then the parents are best treated as belonging to different species.

When these principles are applied to the *Zosterops* described in this study the conclusions reached as regards the specific limits cut right across previous classifications, which have been on a purely "morphological" basis, in fact on colour. Now, though admittedly evidence of intergradation is not as complete as could be wished, the following are the logical deductions :

(1) The yellow *senegalensis* of West Africa is conspecific with the darker (more greenish) birds of Sierra Leone and Liberia (*demeryi*), of the wet area round the head of the Gulf of Guinea (*stenocricota*), and of southern Uganda (*stuhlmanni*).

(2) Darkening further, both eastwards and westwards, *stuhlmanni* is conspecific, via the Yala birds, with *jacksoni* of the western Kenya Highlands and

certainly intergrades with (*a*) the smaller birds (*toroensis*) of Bwamba–Ituri on the eastern edge of the Congo basin and (*b*) with the larger birds of Ruwenzori, Kivu and the mountains north-west of Lake Tanganyika (*reichenowi*), which are among the darkest and greenest in Africa.

(3) West and south through the southern Belgian Congo, *reichenowi* intergrades with the yellower *anderssoni*, of the southern tropical belt, some representatives of which are very like some from the north of the equator. Through central Angola the yellow *anderssoni* intergrades with the large dull *quanzae*, and this, north-eastwards through northern Angola and south-western Belgian Congo, with the smaller and yellower *kasaica*.

(4) The varied birds, some yellower and some greener (usually called *anderssoni* and *stierlingi*) of Nyasaland and south-western Tanganyika Territory (north to Uluguru and Usambara) form a special case. There is no proof of intergradation on any particular mountain in Nyasaland, but (*a*) different areas between them produce a complete series of intermediates, (*b*) local trends in colour can be traced through the highlands southwards from Iringa. Moreover on the Imatong group of mountains, isolated by many hundreds of miles from the *anderssoni-stierlingi* complex, there are indications of intergradation from yellow West African *senegalensis* to greener birds that are indistinguishable from Nyasaland *stierlingi*.

(5) The dull-coloured birds of the south-eastern Abyssinian lowlands and Italian Somaliland (*jubaensis*) intergrade southwards through Kenya and Tanganyika to the larger, more yellow-green, *flavilateralis*.

The relationship of (4) to (1)–(3) remains to be discussed, together with the other outstanding problems in north-eastern Africa, Kenya, Tanganyika and South Africa. Thus, on the basis of the foregoing, two distinct groups, each of intergrading forms, are established at the outset :

Z. senegalensis, including all the *Zosterops* from Senegal to western Abyssinia and south through western Kenya and central Africa to southern tropical Africa.

Z. jubaensis, southern Abyssinia to central Tanganyika.

The fact that belly-colour is not necessarily a specific criterion leads not only to the acceptance of the South African forms *capensis-atmorii* and *virens* as conspecific, which seems proved by the extensive interbreeding, but also to the following conclusions, for which such evidence is lacking :

(6) In the Abyssinian highlands, the yellow-bellied *kaffensis* is conspecific with the grey-bellied *poliogastra*.

(7) In the Abyssinian lowlands, the grey-bellied *abyssinica* and *omoensis* are conspecific with the yellow-bellied *jubaensis* (and hence with *flavilateralis*, extending south to central Tanganyika).

(8) In Kenya and Tanganyika the grey-bellied *kulalensis*, *silvana* and *winifredae* are conspecific with the yellow-bellies on the neighbouring mountains, *jacksoni*, *eurycricota* and *mbuluensis* respectively.

Because interbreeding between the following contiguous forms is at most rare, the following groups are regarded as specifically distinct from each other :

(9) South African *virens* from the *senegalensis* (*anderssoni*) group with which it interdigitates near Mozambique. This conclusion is reached in the face of the fact that in plumage some South African specimens are extremely like some from the Nyasaland mountains (allocated in (5) above to *senegalensis*), but is supported by the small but constant difference in tail/wing ratios.

(10) Highland Abyssinian birds, group (6) above, from lowland, group (7).

(11) Lowland *abyssinica-flavilateralis*, group (7), from the various populations which they surround on the mountains of Kenya and northern Tanganyika.

(12) (West African) *senegalensis* from the *abyssinica* forms, group (7), that it overlaps round Lake Tana.

(13) *Z. pallida*, of south-western Africa, from the *virens* group (9), with which in parts of the Transvaal it is in every respect sympatric. Specific separation of *pallida* is supported by the peculiar relation between its dimensions and the environment.

The foregoing conclusions leave unsolved, and indeed help to produce, the problem of the specific allocation of the montane *Zosterops* of East Africa and Abyssinia. In the first place, it has been throught best to regard the *Zosterops* of Mbulu, Kilimanjaro, North Pare, Chyulu and Teita (Map 6) as conspecific with each other and with the *Zosterops* of the eastern Kenya highlands—that is, *mbuluensis*, *eurycricota* and *silvana* with *kikuyuensis*. The last form has been shown to meet *jacksoni*, typically of the western Kenya highlands, on the north end of the Aberdares, in circumstances that suggest they are not conspecific. However, the birds of South Pare (*winifredae*) share characters of *mbuluensis* on the north and of Usambara birds on the south, in such a way that they all seem to be conspecific. Thus at three removes *kikuyuensis* would be conspecific with the very different-looking Usambara birds, which we were forced (see (4) above) to regard as representatives of *stierlingi* and hence as conspecific with *senegalensis*. This last is the same conclusion as was reached for *jacksoni* in (2) above. It follows that both *jacksoni* and *kikuyuensis*, believed though they are to meet without hybridizing, would both be of *senegalensis* stock. However, their derivation would be at so many removes and by such divergent routes that they might well behave to each other as members of separate species—*cf.* the Great Tits, *Parus major*, of eastern Asia (Mayr, 1947).

A further question is the status of the Abyssinian highland birds (group 6 above). They, too, have a high beak/wing ratio and their yellow-bellied form is so like Kenya highlands birds that it is difficult to believe that it is specifically different. Moreover, there is no difficulty in postulating colonization of the Abyssinian highlands from those of Kenya. This would make also the Abyssinia highlands birds conspecific with *senegalensis*, the nominate form of which impinges on them near Lake Tana. In this case the two forms concerned are so dissimilar in colour, size and proportions, that interbreeding would be most unlikely, whether they are anywhere genetically sympatric or not.

An alternative solution of the East African montane problem would be to make a specific cut, not warranted on morphological grounds, between the South Pare *winifredae* and the North Pare *mbuluensis*. This last, with *eurycricota* and *silvana*, would then form with *kikuyuensis* a polytypic species distinct from *senegalensis* (and *jacksoni*). This would raise a new problem—which species should the Abyssinian highland birds be attached to?

On the whole it seems preferable to adopt the first solution. The specific arrangement of the continental birds is, then, the following, as sketched in Map 1, all the species being polytypic except the first. *Z. pallida* occupies part, *Z. virens* the remainder, of South Africa, *Z. abyssinica* the lowlands of north-eastern Africa, *Z. senegalensis* the whole of the rest of Africa, being purely highland from Tanganyika to Abyssinia.

In considering the relationship of these continental species with those elsewhere there are, as usual in such cases, no guides except morphological characters. In fact with these *Zosterops* no logical solution is possible. On the one hand, there is no compelling reason, morphological or other, to follow current practice and keep either Madagascar or Indian birds as species distinct from African, but for convenience the present arrangement is certainly better maintained. Again, it seems reasonable to keep the *Zosterops* of São Tomé and Principe as a separate species, but their only important character is that they have so much less yellow pigment than their mainland neighbours. In the Indian Ocean also the distinctive Pemba *Zosterops* (*vaughani*) is better kept as a species than attached to *senegalensis* on chance, but there is no objection to this being done with the less distinctive *kirki* of Grand Comoro. *Z. mouroniensis* must, since it occurs in the same small island, be treated as a monotypic species, though its difference from *kirki* is no greater than that between typical *senegalensis* and a dark *stuhlmanni* (from near Lake Victoria). A different problem is posed by the red-flanked birds of Mayotte and of the Seychelles. Though they are separated by hundreds of miles of ocean, the extreme peculiarity that they share qualifies them as conspecific. Again, each of the species on Mauritius (*curvirostris* and *borbonica*) has a representative on Réunion. Finally, the peculiar grey *modesta* of the Seychelles must be kept as a monotypic species.

At the generic level the only separation maintainable is for the four highly aberrant birds in the Gulf of Guinea (*Speirops*).

Considerations of space make it impossible to embody the foregoing views in a formal classification in this study, which is in any case primarily one of variation, but the classification is to appear in the appropriate volume of Peters' *Check List of the Birds of the World*. It will use only those trinomials which appear in the sectional summaries of Parts 4 and 5 above.

Any discussion of the way in which the present state of these Zosteropidae came about could only be speculative and is better avoided. Even if the above view of the birds' relationships is sound, we know too little about the geological and climatic history of the African continent (Moreau, 1952), we do not know whether the first African *Zosterops* was evolved in the continent or was an invader from the east, and finally we have no idea at what stage in Tertiary history the family appeared in a recognizable form. Points of general interest are the marked variation, even though only subspecific, on East African mountains that are very close together, and the widely different types of divergence that characterize the insular Zosteropidae of the Gulf of Guinea and the Indian Ocean respectively.

Although the history of the western Zosteropidae remains inscrutable, the attempt to elucidate their relationships has a value of its own because it has brought into prominence a number of important evolutionary principles. The African *Zosterops* turn out to be a case in which, from the biological view-point of the species, the "morphological" criteria prove to be thoroughly fallacious: there is reason to believe that some of the most dissimilar birds are the most closely related and that some of those which look most alike belong to different species. Moreover, thanks especially to the statistical analyses, it has been shown that correlation takes place in relation to environmental factors to a hitherto unsuspected degree, in a manner that is both direct and highly complicated. Finally, these Zosteropidae provide outstanding examples of the manner in which birds may respond to insular life and among them beautiful and varied cases of "double invasion" of small islands.

SUMMARY

The Zosteropidae occurring in the Ethiopian Region and on Indian Ocean islands are discussed. A main difficulty in their classification has always been the delimitation of the species. This has hitherto been based almost entirely on shade of plumage, but the group is one in which morphological characters are particularly fallacious. Trinomial nomenclature is regarded as a troublesome expedient to be used primarily as a clerical convenience and sparingly.

The colour of *Zosterops* plumage often conceals pigment differences. Microscopical examination has shown that, in accord with Gloger's rule, dry-country populations usually have only brown melanin, though populations with only black melanin occur in all climates. But South African birds carry both types of melanin, and within what has always been regarded as a single subspecies the individuals in drier localities have a higher proportion of brown pigment than those in more humid.

The absence or presence of yellow pigment on the belly is regarded as not necessarily a specific character, as hitherto accepted in the classification of African *Zosterops*, but seems to have a simple genetical basis.

Wing-length in the continental birds is found on statistical analysis to be correlated positively and independently with increase in altitude, with reduction in minimum temperature of cool season and also with rise in maximum temperature of hot season. (The altitude-effect is presumably through the reduced air-pressure.) These results are discussed so far as is possible in the absence of data on weight. The minimum-temperature effect is in accord with Bergmann's rule but the maximum-temperature effect is not, and it is difficult to suggest how it operates. Tail-length and beak-length are closely correlated with wing-length, and, moreover, the tail/wing ratio increases as the wing lengthens. This seems to be correlated with minimum temperature and may be merely one aspect of the general lengthening of body plumage. While in these various correlations certain populations are somewhat aberrant, there are no discontinuities in bodily proportions so striking that they are cogent arguments for specific distinction.

The variation that takes place in the *Zosterops* of Africa is described in six geographical sections. But much of it is clinal, in close correlation with climatic factors, and convergences take place. Finally, on "biological" grounds, it is provisionally concluded that most of the *Zosterops* of Africa belong to a single polytypic species, which includes some of both the lightest (yellowest) and the darkest (greenest) birds. In East Africa this species becomes purely montane, islanded in another species; and the montane populations, though all occupying similar environments and separated by only a few miles, consist of several that differ strikingly in plumage.

The Gulf of Guinea insular Zosteropidae show several examples of double invasion, with gigantism and various other divergences from the normal. The *Zosterops* of the Indian Ocean islands are on the whole less aberrant, showing no tendency to gigantism, even among "first invaders", and the most peculiar are the Mascarene species.

Information about the past history of the Zosteropidae and of the geography and ecology of the terrain occupied is altogether insufficient for the origin of the present situation to be discussed.

APPENDIX 1

MISCELLANEOUS NOTES

NOTE 1. The following are examples of what appear to be slight, but confusing, changes in plumage colour of *Zosterops* specimens.

(*a*) Before describing the *Zosterops* of the Chyulu mountain forests as *chyuluensis*, van Someren referred a series to me for my opinion as to their distinctness from *Zosterops* of other neighbouring mountains. I had no hesitation in agreeing with his view that the Chyulu birds merited a separate name. Now that the specimens are some twenty years old, however, they look so like the neighbouring *mbuluensis* that when series are mixed not all of them can be separated (on slightly darker plumage).

(*b*) Lynes (1934) separated his birds from the contiguous highland areas of Iringa (*ca.* 5,500 ft.) and Njombe (*ca.* 6,500 ft.) into *Z. senegalensis niassae* and *Z. virens stierlingi* respectively. All that can be said of his specimens today is that on the whole the latter series averages a trifle darker than the former.

(*c*) Gyldenstolpe (1924) named all his series from Kivu *scotti* except a single one from the lake shore, which he kept as *reichenowi*. To-day I cannot pick out that specimen from the others.

NOTE 2. Two birds of ordinary *Zosterops* type, but devoid of yellow pigment, were described by Tristram from Madagascar. *Z. praetermissa*[1] owed its appearance to soaking in alcohol (A. & E. Newton, 1888), but the other, *Z. hovarum*, has been universally accepted as naturally grey. The type of the latter cannot now be found in the Liverpool Museum (Mr. R. Wagstaffe, *in litt.*), but Delacour (1932), who examined it about that date, stated that it differed from *Z. maderaspatana* in nothing but colour. There is, then, no reason to believe that *hovarum* was anything but an individual abnormality. It is curious that while the Newtons (*op. cit.*) stigmatize the plate of *hovarum* in *Ibis*, 1887, as inaccurate (they do not say in what respect), Delacour (*op. cit.*) comments that " la planche de l'*Ibis* le represente très exactement ".

Probably another such individual abnormality is the type of Büttikofer's *Z. obsoleta*, a unique specimen with the same dimensions and locality as *Z. demeryi*. The upper surface is given as ashy grey with a very faint olivaceous tinge and the whole lower surface dirty white. From South Africa there is a sight record (Urquhart, 1954) of a *Zosterops* with a " typical white eye ring " but the " entire plumage black ". It is not know whether the usual yellow pigment was present, masked by the excess melanin, or not.

Partial asymmetrical loss of yellow pigment, which has in at least some of the specimens been shown not to be an artifact (Dr. A. J. Marshall, *in litt.*), appears in individuals of four different forms in the British Museum, from Anjouan Is., Grand Comoro, Southern Rhodesia and the Orange Free State. Van Someren (1916) reported a more elaborate abnormality in a Uganda bird, " a greyish mantle and a wide buff-coloured band across the chest ".

NOTE 3. In the beautifully graded series of presumed hybrids between the yellow *gallio* and the grey *buxtoni*, which Dr. G. C. A. Junge has kindly lent me from Leiden, there is the widest possible range of intermediate variation, which seems clearly multifactorial. Here the two parent forms, with bellies that are light clear grey and bright yellow respectively, should certainly provide hybrids obvious on inspection. Nevertheless, intermediates are by no means all easy to detect on colour and the slight size-difference between *buxtoni* and *gallio* ; the nature of most intermediates showing any grey is clear, but specimens from the *gallio* end of the series of intermediates are more difficult. Here it is necessary to assess the differences in intensity

[1] The word *Zosterops* is treated throughout as feminine (see *Bull. Brit. Orn. Cl.* **75** (1955) : 44).

of yellow, an operation often difficult in the museum (and far more so in the field). In fact the first series sent on loan from Leiden contained only intermediates of yellow types and both Dr. Cain and I felt that the evidence for their intermediacy was not very cogent. All doubts disappeared when the birds towards the grey end of the series could be assembled with them.

NOTE 4. Zedlitz (1911 : 56) thought his bird shot in March at the sources of the Mareb was a young *poliogastra* in full winter dress and noted that it was hardly distinguishable from *abyssinica* in full breeding dress. There seems, however, to be no evidence for any such marked seasonal differences as Zedlitz suggested. Thanks to a loan from Stockholm Museum I have been able to examine the specimen in question. It is sexed as male juv., a point that cannot be checked, especially at the whole back of the skull seems to be missing. With wing 56, tail 40, the bird is within the size-range of *abyssinica* but is too small for *poliogastra*, and its beak is brown, a colour strictly characteristic of the *abyssinica* of Eritrea and Abyssinia. On the other hand, the bird shows an approach to *poliogastra* in being slightly greener than most *abyssinica* (and particularly than the two that Zedlitz shot a few days before), in having a little more yellow on the forehead (but not as much as in typical *poliogastra*) and in having the yellow on the throat stronger than it is in *abyssinica*.

NOTE 5. Neumann described *schoana* (type-locality Abuye, Shoa, N.W. of Addis Ababa) as differing from *kaffensis* in having duller upper parts, less yellow on the belly and narrower eye-ring than the yellow-bellies further south (*kaffensis*). On the whole the specimens in the British Museum support this, but better series, well prepared, are desirable. The four specimens available from Dangila and Wanbera (S.W. of Lake Tana) are rather intermediate. Mr. C. M. N. White, who kindly examined these specimens with me, agrees. For simplicity of discussion in the text all the highland yellow-bellies are referred to as *kaffensis*.

Friedmann (1937) showed the range of *schoana* as extending far to the south-east, across the Rift Valley, but there appears to be no basis for this extension. He agrees (*in litt.*, 1951).

NOTE 6. Neumann (*Bull. Brit. Orn. Club*, **21** : 60) claimed that the northern *poliogastra* (type-locality Simien, north of Lake Tana) have no more yellow on the head than a superciliary stripe, while those further south have yellow foreheads, and on this " distinction " he described *erlangeri* from Gadat in Gofa. He claimed that the " superciliary stripe " is much exaggerated in the coloured plate of *poliogastra* (*Ibis*, 1861), which is in fact altogether too brightly yellow and clear grey, but he used the term " superciliary " mistakenly, instead of supra-loral.

It appears that Neumann did not allow sufficiently for individual variation. It is true that a Simien specimen (lent me by the Leiden Museum) has very little yellow on the forehead, but the whole plumage is abnormally deep olive green. Other northern birds, e.g. from Eritrea and Dongolo, have as much golden yellow on the fore part of the head as any in the south of Abyssinia. I conclude, as did Ogilvie-Grant (1913 : 595), that there is no consistent geographical variation in the plumage of *poliogastra* and that *erlangeri* is a synonym.

NOTE 7. The locality " Keren " for *abyssinica* in Zedlitz (1911), and for *senegalensis* (" *aurifrons* ") in Reichenow (1903), may not be critically exact. But Bahr Dar at the south end of Lake Tana has been given by Moltoni (1940) for both *senegalensis* and *abyssinica* and, moreover, the British Museum has a specimen of *senegalensis* from the Unfras R., which is only a few miles away along the shore.

NOTE 8. In the British Museum series of *omoensis*, southwards from the northernmost point of the Omo R., the underparts vary from nearly white with yellow wash on the middle line, to pale grey washed isabelline, and almost pure grey. Kunkur birds (coll. Cheesman) are greyer, not so yellow-green on the back as any of the nine other *omoensis*, and are purer darker grey below than any others available. Yet Amadon *in litt.* reports that one of them agrees well with the type of *omoensis*. The habitat of the Kunkur birds is not certainly known ; the area is covered with acacia woodland, having evergreen trees along stream-beds (Cheesman, *in litt.*).

NOTE 9. Definite localities for *abyssinica* in Somaliland are none of them south of the mountain backbone, about 10° N., and the most northerly locality for yellow-bellies is Sillul, 8° 40′ N. But Oustalet (1886) records a yellow-bellied *Zosterops* (under the name *Z. tenella*) collected by Revoil as " capturé dans les pays Çomalis ". The route map in Revoil (1882) shows that his journeys were all north of 10° 20′ N., but since they extended to the Indian Ocean south of Cape Guardafui his *Zosterops* may have come from further east than the range of *abyssinica*, which is not known from beyond Warsangli.

Revoil's specimen is still in the Paris Museum. It is a very small (unsexed) bird, wing 51, tail 33, with plumage that is brighter and yellower than the yellow-bellies further west towards Lake Rudolf.

NOTE 10. Sclater (1930) thought that *leoninus* (*demeryi*) occurred also in Southern Nigeria, apparently on the evidence of a specimen in the British Museum from Agoulerie, just east of the lower Niger, at about 6° 25′ N. Actually this bird is not as dark as Sierra Leone and Liberian specimens. Moreover four specimens kindly collected on my behalf by Dr. W. Serle at Enugu, only forty miles east of Agoulerie and with rainfall 70 in. (but outside the forest), are typical, " yellow ", *senegalensis*. At the same time, the Lagos population (rainfall also 70 in.) may well be dark ; a single, unsexed, specimen, B.M. 1953.2.50 recently received from there, is peculiarly dull and grey. It looks like an immature, but its skull is hard.

Bannerman (1948 : 124) quoted four authors, Fairbairn, Marchant, Foulkes-Roberts and Brown, as having " reported " *leoninus* from various localities in Southern Nigeria, but as no relevant specimens could be found I made personal inquiries. All four authors have been good enough to reply and it appears that only one (Fairbairn) had collected a bird, which was, however, not authoritatively compared or kept.

In the result, there is no thoroughly satisfactory evidence that dark *Zosterops* occur in coastal Nigeria, but they are certainly to be expected in the high-rainfall belt in the extreme south, perhaps as far west as Lagos. If so, it may well be that they resemble not so much the Liberian birds far to the west, but the more strongly pigmented birds (which have been called *pusilla*) known to occur just on the eastern border of Nigeria, in the Cameroons.

NOTE 11. The lowland localities south and east of Cameroon Mt., from which I have seen small richly coloured birds are Oyem, Bitye, Efulen, Lolodorf, Sangmelima, Mbigou and Mbaika (the type of *pusilla*), i.e. all south of 4° N. It is most unfortunate that there is a lack of well-prepared material from the country just north of this, where the rainfall decreases rapidly and a transition to the yellower *senegalensis* would be expected to correspond. Two birds in poor condition from Bosum, 6° 20′ N., 16° 25′ E., including the type of *savannae*, show some approach to *pusilla*, but one from Kangala, 6° N., 14° 3′ E., shows less. Good (1953) has referred birds from Tibati (about 6° N., 13° E.) and Mboula to *stenocricota* (with which *pusilla* must be synonymized), but his description of their entire underside as " bright light yellow " shows that he is under a misapprehension as to the characters of this form. Thanks to the Chicago and Pittsburgh Museums I have been able to examine three of Good's specimens from these localities. All are much nearer *senegalensis*, having only a trifle more melanin.

NOTE 12. In northern Uganda I have seen skins from Kitgum, Yeilo (N.E. of Kitgum) and Gulu (three). They average wing 55·9, tail 39·8. The Kitgum bird and two of the Gulu are greener than typical *senegalensis*. Two birds from Kibusi Hill, Lango, 1° 54′ N., 32° 44′ E., north of the western end of Lake Kioga, are also intermediate in colour. Again, of four specimens from about 5,500 ft. on the lower slopes of Mt. Debasian (1° 50′ N., 34° 45′ E.) three are not quite so green as lakeside birds.

NOTE 13. South of Lamu and Mongeya the only specimens known from within a hundred miles of the Kenya coast are four males collected in 1900 by Doherty in the " hills 10 miles west of Mombasa " (Carnegie Mus., Pittsburgh). These hills, barely 1,000 ft. high, still have vestiges of a comparatively rich, semi-evergreen vegetation and, as Friedmann (1937) has remarked, all four birds have plumage unlike any others from East Africa. They are greener, less grey, above than the birds north of the Juba, but at the same time the whole of their underside is duller, with paler yellow on the throat and more green on the flanks. Indeed in plumage, though not in size, these Mombasa birds resemble the dull birds of the Angola highlands more than any others. Compared with others in eastern Africa they suggest the mountain forest birds of the Usambara, with both melanin and carotenoid reduced, rather than the *flavilateralis* of the Kenya savanna country. It seems possible that these Mombasa birds belong to a small population sedentary on the ecological island of these hills ; and if so it is regrettably possible that it may have been wiped out.

No specimen of *Zosterops* from Tanganyika Territory or Portuguese East Africa east of the line Usambara Mts.–Uluguru Mts.–Iringa Highlands–Songea Highlands appears to exist in collections except one from Masasi : but R. M. Bell (*in litt.*, 1951) collected a *Zosterops*, which was not retained, at Liwale, 9° 47′ S., 37° 58′ E., on 16th June, 1940. Although there have been a number of observers in the coastal strip in question I have been able to find no sight records, published or unpublished, except that of Haldane (1946) of a single bird " in thick bush along the Rufiji " River, which must I think be regarded as questionable.

Note 14. A number of small mountains rising to between 4,000 and 5,000 ft. that are eastern outliers of the Kenya Highlands, such as Mutha, Endau and the Kimatheni ridge, remain to be explored : and in northern Tanganyika this applies to Gelai and a few little mountains in northern Masailand west of the Pares. It is surprising that no montane *Zosterops* has been taken anywhere in the south-eastern Kenya Highlands, especially the Machakos district which must have been sufficiently wooded in the " early days". On Sagala Mt. (Ndara) just east of Voi vestigial forest resembling that inhabited by *Z. silvana* on the neighbouring Teita Hills seems to contain no *Zosterops* (A. Forbes-Watson, *in litt.*), although this bird reappears on Kasigau Mt., some forty miles further from Teita.

Note 15. Birds from the Yala River area, from which van Someren described *yalensis*, are hardly represented in the British Museum, but I have been able to examine thirty-seven specimens (nearly all lent by American museums), labelled " Yala R.", Kakamegoes, Kaimosi, Lerundo, Kakamega Road, K'brass and Lucosi. All these except K'brass, which cannot be fixed, are close to 0° 10′ N., 34° 55′ E.—about fifty miles north and north-west of Kisumu. Westwards from this there is a belt of country nearly 100 miles wide from which it seems that no *Zosterops* is known. The Yala birds are variable, but they certainly average yellower above and below, with less deep green on the flanks, than *jacksoni*. Some have sharply defined yellow foreheads like *jacksoni*, others more indefinite foreheads, like *stuhlmanni* of Lake Victoria. When Yala birds are mixed with a series from Uganda and Ruwenzori, and the darkest birds are picked out, they prove to come from Ruwenzori and the Yala ; the lightest are from the Entebbe neighbourhood and the Yala.

Nothing seems to have been recorded of the Yala birds in life except that van Someren in describing *yalensis* mentioned that they were found in " parkland ". This is the habitat in which *stuhlmanni* is often found.

Note 16. The characters by which Hartert (*Nov. Zool.*, **34** (1928) : 207) distinguished *somereni* (Mt. Kenya) from *kikuyuensis* do not hold good, as Friedmann (1937 : 373) has already noted.

Note 17. *Z. kulalensis* is known only from the small series collected by Mr. J. G. Williams. The two females labelled as " subadult " differ noticeably from the males and from the single adult female in the smaller amount of yellow throughout. This is particularly noticeable on the underparts, where the throat is greenish rather than yellow and there is no trace of yellow wash in the centre of the grey belly.

Note 18. Ketumbeine and Longido specimens are generally rather dull in colour, without strongly golden foreheads. A single specimen is known also from Oldonyo Erok, an immature, which is particularly dull-coloured, and has an eye-ring smaller than typical *mbuluensis*. The Chyulu birds (*chyuluensis*) are just distinguishable from *mbuluensis*, on average, having a little less melanin on the underparts, but the name is not worth retaining.

Note 19. I have been able to locate only two of the Bwamba birds on which the van Somerens (1949) based their remarks. They are females (Chicago 199163–4) from 2,500 and 3,000 ft., hardly distinguishable from the Medje birds, but perhaps with a trifle less carotenoid, with less contrast below than the Ituri group of birds and with wings 55 and 56. They are at the top of the size-range of this group and at the bottom of the size-range of *stuhlmanni*—as might be expected for their geographical situation. It may be expected that when a good series from Bwamba can be studied it will be found to be transitional between *stuhlmanni* and *toroensis*, probably with high individual variation.

NOTE 20. Specimens in point are Neave's dark birds from " Bunkeya R." and " near Lufupa R." (near Elizabethville, in the Katanga). Most workers have allocated these individuals to the species *virens*, while all the other birds from Katanga and on its borders, being yellow, were treated as *anderssoni*. Chapin, who has kindly also examined these specimens at my request, agrees that they are best regarded as individual variants.

NOTE 21. These remarks are based on twenty-seven specimens from the highlands (4,170 ft. upwards) and ten from the Vila Salazar–Quicolungo area. Chapin (1954) notes that specimens from Pungo Andongo and Canhoca (i.e. close to the two preceding localities), which I have not seen, are " very like *anderssoni* ", which implies that they have more carotenoid than the highland birds—a finding in agreement with mine. Those referred to by Monard (1934) from Indungu (50 km. S. of Vila da Ponte) and Kalukumbe cannot be traced (Director, Chaux-de-Fonds Museum, *in litt.*). Paris Museum possesses a specimen C.G. 1908 : 487 Mission Vasse labelled " Benguella ", also a fairly large (wing 60), dull-coloured bird, but it is uncertain whether it came from the coast town or from somewhere in the extensive Benguela province (which has included the highlands under discussion). If any *Zosterops* exist on the dry coastal belt of Angola, where the rainfall is as low as 10 inches, it would be extremely interesting to compare them. But none seems to have been recorded from there, nor from the neighbouring north coastal zone of South West Africa.

NOTE 22. Bangs and Loveridge described *sarmenticia* from Igale, in the Poroto and Rungwe Mts. at about 6,000 ft., as larger than *stierlingi*, and more richly coloured, with bigger beaks. I find that the birds from these mountains average barely 1 mm. longer in wing than either the dark Nyasaland birds or the dark birds from the rest of south-western Tanganyika Territory ; and I can see no difference in the beaks. But Poroto and Rungwe birds certainly are a trifle more strongly pigmented than any others, there being a specially rich contrast on the underside between deep green flanks and chrome-yellow centre of belly. Specimens which approach these most nearly come from (*a*) on the south the nearest mountains in northern Nyasaland, Nyankowa, Mugesse (Masukus) and the Nyika, (*b*) Ukinga, just east of Rungwe, and Dabaga, on the wet eastern edge of the Iringa plateau.

NOTE 23. The following names have been given to *Zosterops* in southern tropical Africa : *kasaica* Chapin (1932), from the Kasai, S.W. Belgian Congo ; *quanzae* de Schauensee (1932), (upper) Cuanza R., Angola ; *anderssoni* Shelley (1892), Elephant Vley (extreme northern S.W. Africa) ; *sarmenticia* Bangs and Loveridge (1931), Poroto Mts., S.W. Tanganyika Territory ; *stierlingi* Reichenow (1899), Iringa, S. Tanganyika ; *niassae* Reichenow (1904), Songea, S.E. Tanganyika ; *tongensis* Roberts (1936), southern P.E.A. No difficulties arise about the use of the first two names for the small, richly coloured, birds of the S.W. Belgian Congo and the large, dull, birds of the Angolan highlands respectively.

As stated, south of these the birds of the non-evergreen country extend from the Atlantic to the Indian Ocean, becoming slightly duller and greyer in the south-eastern Belgian Congo, and slightly greener in the east, as Portuguese East Africa and Zululand are approached. For these latter birds the name *tongensis* is available, but since no range could be assigned to it and the difference is so small, it is preferable to retain *anderssoni* throughout. Similarly, this name may be applied to the Songea birds, which cannot consistently be distinguished from Rhodesian. Thus *niassae* also becomes a synonym of *anderssoni* as Mackworth-Praed and Grant (1945) have already concluded.

It remains to decide on a name for the dark birds. The type of *stierlingi*, labelled as coming from Iringa, is a poor specimen, differing from the type of *niassae* only in being a little greener. If it came from the neighbourhood of Iringa township, and not from somewhere else in the then extensive Iringa Bezirk, Lynes's (1933) Iringa specimens are practically topotypes. However, he preferred to call them *niassae*, because they were a trifle yellower than the birds he got further south in Njombe, which he called *stierlingi*.

The most richly pigmented population is that north-west of Lake Nyasa, called *sarmenticia*, East, north-east (including the type locality of *stierlingi*) and south the birds become less dark, but there is no clear geographical cline. The question is whether to retain both *sarmenticia* and *stierlingi*, or only the former (the extreme type but the younger name) or only the latter (an intermediate type but the older name). I follow the last course because :

(*a*) One could not delimit the respective ranges of both *sarmenticia* and *stierlingi*.

(*b*) Birds of intermediate (nearer *stierlingi*) plumage have a far more extensive range than *sarmenticia*, discontinuously (on mountains) to some 700 miles north of Lake Nyasa, as well as down through Nyasaland.

(*c*) The name *stierlingi* has been in more general use than *sarmenticia*.

Note 24. *Z. capensis* has been recorded by Shortridge (*J.S. Afr. Orn. Un.* **1** : 22) as irregular in appearance July–September at Hanover, C.P., which is north-east of Murraysburg, about halfway to the Orange River. As Map 10 shows, there is nothing inherently improbable in this record, but it sounds as if it refers to wandering just before the breeding season. Also no supporting specimen can be found and as the area is a critical one for the mutual ranges of grey-bellies and pales it seems better not to enter it on the map. A *capensis* record that must clearly be rejected is that of Taylor (1907) on the Transvaal–Swaziland border. He purports to have collected it there, but no specimen can be found and the identification must be a mistake. The record of *anderssoni* close to King Williams' Town by Pym (*J.S. Afr. Orn. Un.* **5** : 91) is also dismissed as an error.

Miss Courtenay-Latimer has recorded (*in litt.*) seeing both pale-bellies and greys (*capensis*) on the banks of the Vaal R., about thirty miles north of Kimberley. Further information on the occurrence of the latter form so far from their main range must be awaited.

Map 11 is based on a sketch-map compiled for me by Dr. R. M. Harwin, mostly from unpublished information. Additional records have been incorporated from Mr. J. Last, Dr. G. Rudebeck and specimens in the British and Transvaal Museums. Since Map 11 was drawn it appears that pale-bellies are altogether more uncommon than green-bellies at Pretoria and probably also the more uncommon of the two at Johannesburg. Also Vaals have been reported from Heidelberg.

Note 25. The only (5) specimens from Potchefstroom, Gaberones, Matlapini and Rustenburg are all rather dull and pale. Also, seven specimens recently collected by Dr. G. Rudebeck at Blouberg, at about 23° 00′ S., 28° 55′ E., show the same characters, though only about fifty miles west of the Zoutpansberg, where the *Zosterops* are "normal" *virens*. Although evergreen forest of a dry type occurs in both mountains the Blouberg climate is drier than the other, for the mission stations at its southern foot have mean annual rainfall of only 21·7 and 27 inches compared with 44 at the south foot of the Zoutpansberg.

Note 26. British Museum specimen No. 76.5.23.921, classified as *pallida*, bears a note on the label that it is the specimen listed in *Ibis*, 1869 : 290 as *capensis*. The collector was Ayres and the locality "Transvaal", a country from within 100 miles of which no grey-belly has been authentically recorded. The specimen differs from normal *pallida* in having upper parts darker and more olive, yellow on throat stronger, and entire underparts devoid of whitish. Instead the breast is greyish and the belly the same warm, rusty, brown as the flanks. There is some yellow on the forehead—a characteristic of *pallida* and *atmorii* (but not *capensis*)—and if the locality had been anywhere in the north of the Cape Province the specimen would have been accepted as a hybrid.

Note 27. There has been some inadvertent misrepresentation of these Gulf of Guinea birds in the text and in the figures in Bannerman (1948) :

(1) The measurements (wings 58–62, tails 45–49) ascribed to *Z. f. ficedulina* on p. 130 must be due to a clerical error ; in fact Principe birds are not bigger than the São Tomé (see Part 2 of Appendix 3).

(2) The black of the lores of *griseovirescens* is marked under the eyes, but does not continue behind them as shown in fig. 34.

(3) Fig. 36 of *leucophaea* is misleading : both in the museum and in the field (D. W.

Snow, personal communication) this looks to be a bird with a whitish head, with which the white eye-ring does not contrast.

(4) The Annobon bird is not " the largest white-eye of the genus *Zosterops* ", as stated on p. 131. In Africa it is exceeded by some Abyssinian and South African populations, as shown in Appendix 3.

(5) The green *Zosterops* from Fernando Po, described by Bannerman as *poensis*, is, as Bates (1911), Serle (1950) and Amadon (1953) have all concluded, not distinguishable from the Cameroon Mt. *stenocricota*. The slightly larger dimensions of the Fernando Po birds (compare Part 2 of Appendix 3 with population 21 in Part 1) are unexpected in view of the greater height of Cameroon Mt., but the average altitude from which the available Cameroon birds came is only 4,000 ft. and that of the Fernando Po specimens (which is unknown) may not be comparable.

(7) Colours of soft parts have in the past of necessity been derived from dried specimens, in the absence of details on collector's labels. Data recently provided give :

For *melanocephala* (W. Serle) : beak and legs both fleshy white to creamy white.

For *lugubris* (D. W. Snow) : beak yellow brown, darker above ; legs, flesh.

For *leucophoea* (D. W. Snow) : upper mandible dark grey, lower, whitish ; legs and feet pearl grey with yellow soles.

The beaks of *ficedulina* and *feae* differ markedly in colour, at any rate in the skins, the former being dark horn above, paler below, and the latter whitish tipped blackish.

Note 28. Stresemann (1948) is prepared to keep three of the abnormal birds in *Speirops* but regards the remaining one, *brunnea*, as " closer to the ordinary type of *Zosterops* ". He points out that *brunnea* has a longer tail, more slender beak and different colour pattern from *Speirops lugubris*. In colour, however, *lugubris* differs no less from another *Speirops*, *leucophoea*, and its shortness of tail is a character of some otherwise " normal " *Zosterops*. Also, *brunnea* is so far from being an " ordinary " *Zosterops* that hesitation must be felt about including it in that genus. And, on the whole, in view of the uncertain phylogeny of these Gulf of Guinea birds, no violence is done, and practical convenience is served, by keeping all four abnormal birds in *Speirops*.

It may be added that *Speirops brunnea* is known from only two specimens. The type (not sexed) was described by Salvadori as having wing 62, tail 50. The Berlin bird, also not sexed, Stresemann (1948) reported as having wing 66, tail 54, but on remeasurement (*in litt.*) 65/55.

Note 29. While the brightest *griseovirescens* is only grey-green, some specimens (especially worn birds, including one noted on its label as " nesting ") are so devoid of lipochrome that on the upper parts the green is limited to a tinge on the upper tail-coverts and the under tail-coverts are practically white. There is also much variation in the colour of the belly and flanks, some being a warm brown (correlated with the greener type of upper parts), others very pale.

Note 30. My conclusions about the Madagascar birds, based on the British Museum series, have been reached independently from those of Salomonsen (1934*a*, 1934*b*) and Rand (1936). Although the series I have seen is smaller than that available to Salomonsen, it suggests no such clear distinction in size between *analoga* and the other populations as he thought. It is true that the high-level (Manjakatompo) birds I have measured have wings 59–63 mm. and the smallest *Zosterops* in Madagascar 52–58, but two from Iampasika, at an intermediate level, have wings 59 and 60 and three from lower altitudes elsewhere in the island 59.

Note 31. The plate of *Z. comorensis* in Shelley (1900) is not quite accurate in that it makes the bend of the wing too yellow and shows a sharp demarcation between yellow throat and green side to head. This would be correct for the Madagascar birds, but the *comorensis* skin appears to have ear-coverts and cheeks greenish yellow, not green, and hence not contrasting with the throat.

Note 32. *Z. mouroniensis* seems to be represented by only three very old specimens, two mounted in Paris and one (without collector's name) in Berlin which was at one time mounted, Thus at least one of the four birds collected by Humblot (Milne-Edwards and Oustalet, 1888) is unaccounted for. Thanks to Professor Stresemann I have been able to examine the Berlin specimen. It has upper parts a dingy olive-green, underparts a greyish olive yellow (including the under tail-coverts and thighs). It is altogether much darker and less yellow than as figured in Plate 5 (*ibid.*), but at least some of this effect may be due to age and dirt. Its wing measures 63 mm., tail 45, tarsus 22 (beak damaged). Professor Berlioz has kindly measured the mounted specimens in Paris for me and finds wings 60 and 64, tails 50 and 52. Milne-Edwards and Oustalet (1888) gave wing 66, tail 57. The name of the bird is derived from Mouroni, the (low-level) capital of Grand Comoro, but it is not clear that it was obtained there, as Shelley (1900) states.

NOTE 33. Vesey-Fitzgerald (1940) found no *Zosterops* on Marianne, but specimens in the British Museum show that it persisted there as late as 1888. Its extinction may have resulted from the clearing of the jungle for coconuts that Newton (1867) heard was intended. There appears to be no concrete evidence to support the record of *semiflava* from Praslin Island (15 sq. miles) by Shelley (1900) and Sharpe (1909) : and the mention of *semiflava* by Newton (1867) on Praslin, Silhouette (8 sq. miles), La Digue (4 sq. miles) and Mahé, is in every case tentative or by local report.

NOTE 34. *Z.* (*Malacirops*) *e-newtoni*, described by Hartlaub from Réunion, was not decisively rejected by Sclater. Gadow (1884) may, as A. & E. Newton (1888) claimed, have had inadequate material at that date for his statement that *Z. e-newtoni* and *Z. borbonica* " form a perfect gradation " ; but *e-newtoni* certainly differs only in having its plumage a cold grey throughout, instead of being suffused with brown like *borbonica* ; Berlioz (1946) is convinced that it does not deserve specific status ; and it is incredible that in the island of Réunion there should be two *Zosterops* of identical size and proportions (in addition to *haesitata*). The *e-newtoni* individuals on Réunion in fact are a local abnormality that is more like the allied form, *mauritiana*, on Mauritius. *Pace* Gadow (1888) there appears to be inadequate sexed material to support the view that the female *borbonica* is browner than the male.

NOTE 35. The *Zosterops* of Gloriosa Is., described by Ridgway as *gloriosae*, is represented in the British Museum by six good skins. When mixed with a series from Madagascar they cannot be separated from the yellowest, and their measurements (wings 55–57·5) fall within the range of *maderaspatana*. Nicoll (1906) also concluded that they were indistinguishable and it is not known on what grounds Sclater (1930) retained the name *gloriosae*. Most of the Gloriosa birds have a little yellow wash on the grey belly, and an immature female has most of the underparts washed with gamboge, together with a golden tinge on the lores. No *Zosterops* seems to have been collected on Astove ; the single one from Cosmeledo is a little yellower than Madagascar birds.

NOTE 36. *Z. völtzkowi* was originally described by Reichenow by comparison with *anjouanensis* and *comorensis* (which it seems unlikely that he can have seen), apparently on one skin and four specimens in spirit, which have of course lost all their yellow. However, four specimens obtained recently (1948) by Lt.-Col. Ph. Milon on Europa Is., while showing no consistent difference in colour or wing-length from Madagascar birds, have markedly longer tails.

APPENDIX 2

ANCILLARY CHARACTERS

Iris colour

The only *Zosterops* in which any iris-colour other than brown appears to preponderate are those *senegalensis* which extend in a belt along the southern edge of the Sahara from Senegal to Eritrea. Bates (1930) gives the iris-colour of West African birds as " light grey " and he is supported by the particulars on the labels of most of the B.M. specimens from Cameroons westward ; yet Bannerman (1948) gives " very pale yellowish brown " for West African birds, and Reichenow (1903) " dark red brown ". Certainly the iris-colour of immature birds in West Africa is brown (see especially two immatures from Portuguese Guinea with irises noted by Ansorge as " brown ochre "). Of exceptional adults, W. P. Lowe got a female with " brown " iris at Bathurst, in the Gambia, Shuel a female with " brownish " at Zaria in Nigeria, and Bates himself a male in Bornu with " very light yellowish brown " and a male with " brown " in the Cameroons. At the eastern end of " *senegalensis* " Butler and Lynes recorded iris-colour of Roseires and Darfur birds respectively as grey, while an unsexed bird collected by Bohndorff at 8° N., 26° E., S.S.E., of Lynes' bird, had " full brown " iris and a Kajo-Kaji bird collected by J. H. Miller " hazel ". Again, among the series of Uganda *stuhlmanni*, typically with brown iris, there is one with iris noted as " white ". Still more remarkably, in a series of eight specimens all apparently adult, from Melsetter, Southern Rhodesia, the iris colours are noted variously as yellow, light yellow, grey and brown (of several shades).

Beak colour

Throughout Africa the beaks are black, except in two Abyssinian populations, *omoensis* of the southwest and *abyssinica* of the east, which have the beaks brown. However, the populations of *abyssinica* that live further to the south-east, in Somaliland, and are otherwise similar to the others, have black beaks. All the insular birds of the Indian Ocean also have black beaks ; it is only the otherwise highly aberrant birds of the Gulf of Guinea islands and Cameroon Mt. which have strikingly different beaks—whitish.

Leg colour

All the forms whose leg colour is recorded on labels have it more or less grey—brownish-grey to blue-grey—except two from the Gulf of Guinea that are in other respects highly aberrant (genus *Speirops*). These have pale flesh-coloured legs.

Feathering sequence of the nestling

A peculiar condition of head-feathering has been recorded (Moreau and Moreau, 1939) in nestlings of the Kilimanjaro and the Usambara mountain-forest *Zosterops*, two forms the adults of which are as unlike as any of those belonging to that habitat. Two young Kilimanjaro *Zosterops* about two days before they left the nest had the back, wings and crown fully feathered, but the forehead was only in quill, while " the lores, together with a strip over and under the eye were bare. There was no sign of the white eye-ring, even in quill." Again, in Usambara nestlings which had the feathers on the hinder half of the crown full-grown " the entire forepart of the head was practically naked ". Since no similar records had been traced elsewhere it seemed that this might possibly be a character of taxonomic significance and attempts have been made to learn something of its geographical occurrence.

In Nyasaland Mr. C. W. Benson has kindly given me details of two broods of advanced nestlings regarded as conspecific with Usambara birds. In one brood the retardation of feathering on the fore part of the head was as in the Usambara birds ; but in the other brood feather-sheaths were showing on the lores. Dr. Chapin has recently sent me a nestling from the Kivu which shows a somewhat intermediate condition. It is fully feathered (tail and wings still very short), but the lores and the rim round the eye, which would in the adult be occupied by the white eye-ring, are bare. The only other African *Zosterops* for which I have been able to get any information is the (grey-bellied) Cape Town bird ; Mrs. M. K. Rowan (*in litt.*) has collected information that the head-feathering is complete in the nestling stage.

Delay in head-feathering seems to be widespread in the genus *Zosterops*. Davidson (1952) has noted that young New Zealand *Zosterops* (*lateralis*) on the day before leaving the nest had " a little bare patch on the top of the head and round the eye " ; the photograph of newly fledged birds ascribed to *simplex* (from somewhere in south-eastern Asia) in Schmitt (1931) appears to show the forehead and the surroundings of the eyes as naked. But Mr. E. M. Reid-Henry tells me that lowland Ceylon birds (*palpebrosa*) do not show any bareness. Also two nestling *hypoxantha* (from the Pacific), lent by Prof. Stresemann, have the head completely covered.

More critical observations are needed, but meanwhile it seems that sequence of head-feathering is probably not a useful taxonomic character.

Beaks and tongues

The beak is so readily adaptive that it cannot be expected to be of taxonomic significance. It may, however, be noted that the beaks of all the Zosteropidae under discussion are much alike, irrespective of habitat, except for special elongation in one species inhabiting Mauritius and Réunion. In general, also, the correlation between length of beak and length of wing is remarkably close (Part 3).

In connection with the present study, as many tongues have been examined microscopically as possible, and the result will, it is hoped, be published separately. All show a rather similar degree of specialization, being bifid, slightly folded so as to provide a channel (for nectar and juices), and fimbriated.

Wing formula

In all the Zosterops dealt with in this study, primaries 3, 4 and 5 are the longest, nearly equal, markedly exceeding primary 2 (by up to one-tenth of the wing-length) and somewhat exceeding primary 6. This in most forms is markedly longer than primary 2. (Primary 1 is so reduced in all forms that it does not enter into discussion.)

The biggest differences between primary 2 and primary 3 (up to 6 and 7 mm.) are found in the various highland birds of East Africa and Abyssinia, which might be expected, merely because these are the longest-winged birds. The small birds of south-western Abyssinia (*omoensis*) have, however, nearly as big a gap between second and third primaries. In general, the difference between primaries 2 and 6 varies with that between 2 and 3, though it is consistently smaller. But in each population the individual variation in these respects is great.

Two forms of African *Zosterops* are more blunt-winged than any others : both the pale-bellied birds of south-western Africa (*pallida*) and the yellow birds of the northern savanna (*senegalensis*) have the difference between the second and third primaries as little as 2 mm. in some specimens and the sixth little or no longer than the second.

From the foregoing it appears that wing-formula is not of taxonomic value. Nor does it seem to have a consistent ecological relationship. The two blunt-winged forms cited above both belong to dry country, but the character is less marked in two others of comparable environment, *abyssinica* and *flavilateralis*.

Song

Song is known to be variable in some species of birds (even to the extent of losing locally the specific characters). However, for the *Zosterops* as much information as possible has been assembled, much of it unpublished, from correspondents, in case something helpful should emerge. Especially as verbal renderings of bird-songs are difficult to evaluate, by far the most valuable information comes from the comparisons made of *Zosterops*-songs in different areas made by individual listeners. Thus :

(1) The songs of the two Nyasaland *Zosterops*, highland and lowland, were found by Benson (1948) to be identical with each other and with that of the superficially very different, grey-bellied, bird of the Abyssinian highlands, while he also once heard the same song from a Uganda bird. The four birds concerned have usually been attributed to three different species (four different subspecies).

(2) The Usambara and Kilimanjaro mountain-forest birds, which look as different as any two forms occurring in this vegetation-type, have the same song (personal observations).

(3) The South African birds, green-bellied, grey-bellied and pale-bellied, which in the past have been attributed to two, or three, different species, have all practically the same song (Mr. C. J. Skead ; Mrs. M. K. Rowan).

All the songs referred to above are described as being of Blackcap (*Sylvia stricapilla*) or Garden Warbler (*S. borin*) type and quality. Something of the sort is probably very widespread in the Zosteropidae, for in New Zealand *Z. lateralis* sings like a Hedge Sparrow (*Accentor modularis*)—Mr. E. G. Turbott, personal communication. It is therefore surprising to find that one Kenya form (*Z. kikuyuensis*), occupying mountain forests situated between those inhabited by the birds with Blackcap-type songs cited above, has a very different song—described by Sir Charles Belcher, a very competent observer, as about twenty repetitions of practically the same note. This may perhaps have affinities with the several songs that have been likened by observers to that of the Willow Warbler (*Phylloscopus trochilus*), in Pemba Island (off the East African coast) and on Principe Island (Gulf of Guinea)—as well, incidentally, as in Ceylon (*palpebrosa* but not *ceylonensis* : Mrs. C. Lushington *per* Major W. W. A. Phillips *in litt.*).

For the present purpose all that can usefully be inferred from the foregoing is that among the African *Zosterops* birds of very dissimilar appearance, which have been ascribed to different species, have similar songs. In such cases identity of song would support arguments, put forward on other grounds, that the birds concerned were conspecific, but the song character alone could bear no weight for or against close affinity.

APPENDIX 3

DIMENSIONS, ETC., OF VARIOUS POPULATIONS OF ZOSTEROPIDAE

Notes

(1) Names are taken from Sclater (1930) or subsequent describer, without prejudice to reconsideration. Where no name is given none has been applied to, or covers, the particular population.

(2) " Mean altitude " and " temperature " are obtained as explained in Part 3.

(3) Beak-lengths are not available for certain populations (see Part 3).

(4) Standard deviations in wings are all below 2·5 mm. (only 3 of them exceeding 2·0), in tails all below 3 mm. (18 exceeding 2·0), in beaks all below ·9 mm. (7 exceeding ·75).

PART 1. AFRICAN CONTINENTAL POPULATIONS

Population.		Specimens examined	Mean altitude	Temperature ° F.		Wing-length	Tail-length	100 × tail	Beak-length	100 × beak
No.	Area and name.	No.	a.s.l. (ft.).	Max. (mean)	Min. (mean)	mm.	mm.	wing	mm.	wing
	N.E. TROPICAL AFRICA									
1	Eastern Ethiopian highlands except extreme south (*poliogastra*)	54	8,000	77	46	63·9 (58–69)	48·4 (43–53)	75·7	14·1 (13–15)	22·1
2	Eastern Ethiopian highlands extreme south (round Yavello) (*poliogastra*)	11	6,000	83	50	61·5 (59–63)	47·3 (46–49)	76·9	14·1 (13–15)	22·9
3	Western Ethiopian highlands, north of Addis Ababa–Nono (*schoana*)	14	8,000	77	46	63·2 (61–65)	48·7 (45–50)	77·1	14·7 (14–16)	23·3
4	Western Ethiopian highlands Addis Ababa–Nono southwards (*kaffensis*)	29	6,500	82	48	60 (57–63)	45·1 (41–48)	75·0	14·0 (13–15)	23·3
5	S.E. Sudan and E. Eritrea below 5,000 ft. (*abyssinica*)	15	3,500	96	60	54·4 (52–56)	38·4 (36–42)	71·1	12·9 (12–14)	23·7

Population. No.	Population. Area and name.	Specimens examined. No.	Mean altitude a.s.l. (ft.).	Temperature ° F. Max. (mean)	Temperature ° F. Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
6	Ethiopia, eastern dry country (*abyssinica*)	16	4,500	89	57	58·3 (54·5–60)	41·8 (38·5–45)	72·0	13·3 (12–14)	22·9
7	British Somaliland (*abyssinica*)	21	4,000	86	52	57·1 (55–60)	41·9 (39–46)	73·4	13·4 (12·5–15)	23·5
8	S.W. Ethiopia lower ground (*omoensis*)	11	4,000	93	59	55·7 (54–57)	39·0 (35–41)	70·0	12·7 (12–13)	22·8
9	Imatong group of mountains, Sudan - Uganda border	14	7,000	83	47	60·0 (58–62)	42·2 (39–48)	70·0	13·3 (12·5–14)	22·1
10	Round N. end Lake Rudolf (*jubaensis*)	11	2,000	94	70	52·1 (50–54)	34·3 (32–38)	65·8	12·2 (11·5–12·5)	23·4
11	East of population 10 (lower ground S. of Yavello; (*australoabyssinica*)	14	4,500	86	61	53·6 (52–56)	36·6 (35–39)	68·3	12·1 (11–13)	22·6
12	Italian Somaliland (*jubaensis*)	17	500	98	72	51·8 (50–54)	34·2 (31–37)	66·1	11·5 (11–12)	22·2
	West Africa and Sudan									
13	Liberia and Sierra Leone (*leoninus*)	14	500	91	68	52·8 (51·5–54)	35·1 (33–37)	66·6	11·8 (11–13)	22·3
14	Gold Coast westwards except area 13 (*senegalensis*)	18	500	94	66	53·5 (51–55)	35·6 (33–37)	66·3	12·4 (11·5–13)	23·2
15	Nigeria and Cameroons below 3,500 ft., north of 8° N. (*senegalensis*)	23	1,500	98	63	55·9 (53–59)	37·5 (35–40)	67·1	12·2 (11–13)	21·8
16	Nigeria and Cameroons below 3,500 ft. 8°–4° 30′ N. (*senegalensis*)	19	1,500	88	67	53·7 (51–57)	36·0 (34–39)	67·0	12·5 (11·5–13)	23·1

Population.		Specimens examined	Mean altitude	Temperature ° F.		Wing-length	Tail-length	100 × tail	Beak-length	100 × beak
No.	Area and name.	No.	a.s.l. (ft.).	Max. (mean)	Min. (mean)	mm.	mm.	wing	mm.	wing
17	Sudan north of 8° N. (*superciliosus*)	15	2,000	100	62	56·1 (54–58)	38·3 (36–40)	68·5	12·6 (12–13)	22·5
18	Sudan and N.E. Congo 8°–3° N. (*superciliosus*)	25	2,000	94	64	54·6 (52–59)	37·3 (35–41)	68·3	12·3 (11–13)	22·5
19	Bamenda highlands (*stenocricota*)	24	6,000	82	59	58·7 (56–61)	38·6 (34–41)	65·5	13·5 (12·5–14·5)	23·0
20	Manenguba group of highlands	9	4,000	84	64	53·1 (51–55)	31·2 (30–34)	58·2	12·7 (12–13·5)	23·9
21	Cameroon Mt. (*stenocricota*)	13	4,000	89	69	54·2 (52–57)	33·4 (31–35)	61·6	12·1 (11·5–12·5)	22·3
22	Cameroon Mt. (*melanocephala*)	21	8,000	65	46	63·0 (61–65)	43·2 (41–47)	68·6	15·0 (14–15·5)	23·7
23	S.E. of Cameroon Mt. to 1° N. and 3° E. (*pusilla*)	12	1,000	89	69	51·3 (49–53)	31·5 (30–33)	61·4	12·5 (12–13)	24·3
	EAST AFRICA									
24	Eastern Kenya below 4,000 ft. (*flavilateralis*)	53	2,300	88	65	53·8 (51–57)	35·7 (32–39)	66·3	12·0 (11–13)	22·3
25	Eastern Kenya, dry country 4,000–6,000 ft. (*flavilateralis*)	32	5,000	83	55	55·4 (50·5–59)	37·8 (35–41)	68·2	12·2 (11–13·5)	22·0
26	Tanganyika Territory, dry below 4,000 ft. (*flavilateralis*)	34	2,500	86	60	54·3 (52–57)	36·0 (35–39)	68·0	12·2 (11–13)	22·5
27	Central Tanganyika, dry 4,000–6,000 ft. (*flavilateralis*)	30	5,000	82	53	55·2 (53–58)	38·3 (35–41)	69·2	12·2 (11–13)	22·1
28	Kulal Mt., N. Kenya (*kulalensis*)	8	6,000	81	50	62·7 (61–64)	46·5 (45–51)	74·2	15·4 (14–16)	24·6

Population.		Specimens examined.								
No.	Area and name.	No.	Mean altitude a.s.l. (ft.).	Temperature ° F. Max. (mean)	Temperature ° F. Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
29	Marsabit Mt., Kenya	12	4,000	80	57	57·5 (56–60)	41·0 (39–42)	71·3	12·8 (12·5–13)	22·2
30	Laikipia plateau, Kenya	7	6,700	79	46	62·6 (60–64)	47·0 (43–51)	75·1	13·7 (13–14)	21·9
31	Mt. Kenya 9,500 ft. upwards (*kikuyuensis*)	23	10,000	69	40	62·0 (59–66)	47·6 (43·5–50)	76·8	13·9 (13–15)	22·4
32	Rest of E. Kenya highlands (*kikuyuensis*)	95	7,500	76	46	60·6 (56·5–64)	46·4 (42–51)	76·6	13·7 (12–15)	22·7
33	Chyulu Mts., Kenya (*chyuluensis*)	14	6,000	81	50	62·0 (59–65)	47·9 (45·5–52)	77·3	14·5 (13·5–15)	23·4
34	Teita Hills, Kenya (*silvana*)	33	5,000	82	53	58·1 (56–63)	45·7 (43–49·5)	78·6	14·5 (13·5–16)	24·9
35	Kilimanjaro group (*eurycricota*)	46	6,000	80	49	61·1 (59–64)	47·7 (43–50)	78·1	14·2 (12·5–16)	23·2
36	N. Pare Mts., Tanganyika Territory (*mbuluensis*)	14	5,500	82	51	60·4 (58–63)	45·1 (40–48)	74·7	14·2 (13·5–15·5)	22·7
37	Mbulu group of mountains, N. Tanganyika (*mbuluensis*)	37	6,500	78	48	62·5 (60–67)	47·5 (43–53)	75·9	14·7 (13·5–16·5)	24·3
38	S. Pare Mts., Tanganyika Territory (*winifredae*)	12	5,500	82	51	59·1 (58–62)	43·3 (41–46)	73·3	13·7 (13·5–14)	23·2
39	Mt. Elgon, N.W. Kenya (*jacksoni*)	45	(7,000)	78	49	60·6 (58–65)	46·0 (42–51)	75·9	13·7 (12·5–15)	22·6
40	Western Kenya highlands between Elgon and Naivasha (*jacksoni*)	68	8,500	73	43	62·0 (57–67)	46·4 (42–50)	74·8	13·9 (13–16)	22·4
41	Western Kenya Highlands Naivasha–Loliondo (*jacksoni*)	17	7,000	75	48	60·6 (57–65)	46·6 (40–49)	76·9	13·5 (13–14·5)	22·3

Population. No.	Population. Area and name.	Specimens examined No.	Mean altitude a.s.l. (ft.).	Temperature ° F. Max. (mean)	Temperature ° F. Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
42	Kavirondo, W. Kenya (*yalensis*)	38	4,500	86	58	58·3 (56–62)	42·3 (39–46)	72·5	13·2 (12·5–14)	22·6
43	Ukerewe Is., L. Victoria	11	4,000	83	62	58·8 (57–61)	43·9 (42–45)	74·7	12·4 (11·5–13)	21·1
44	Uganda below 5,000 ft. (*stuhlmanni*)	49	4,000	85	60	58·1 (55–62·5)	41·3 (37–44)	71·1	13·0 (12–14)	22·4
45	Ruwenzori (over 5,000 ft.) (*stuhlmanni–scotti*)	67	6,900	75	50	60·2 (56–63)	44·5 (41–49)	73·9	13·4 (12·5–15)	22·2
46	Ruwenzori, western foot-hills	37	4,000	86	60	57·9 (54–61)	41·3 (36–47)	71·3	12·7 (11·5–13·5)	21·9
47	Bwamba – Ituri – Beni, N.E. Belgian Congo (*toroensis*)	18	3,000	89	63	53·7 (51–56)	36·9 (34–40)	68·7	12·3 (11·5–13)	22·9
48	Highlands W. of L. Edward to 5,000 ft.	31	4,700	80	57	57·1 (54–60)	40·6 (37·5–44)	71·5	—	—
49	Highlands W. of L. Edward 5,000–8,500 ft.	10	6,800	73	51	61·5 (58–65)	46·6 (45–50)	75·7	—	—
50	Kivu volcanoes.	32	9,500	65	41·5	62·5 (59–65)	47·9 (43–51)	76·6	13·9 (13–15)	22·2
51	Kivu, lower levels	44	6,000	77	53	60·7 (58–64·5)	45·4 (40–50)	74·7	13·3 (12·5–14)	22·0
52	Mountains N.W. of Lake Tanganyika (*reichenowi*)	22	7,000	73	50	61·4 (59–64)	45·3 (41–50)	73·8	13·7 (13–14)	22·3
53	Kakanda, 40 miles west of preceding (52)	14	4,300	82	60	55·9 (54–58)	39·1 (37–41)	70·0	—	—
54	Kamituga, 25 miles west of preceding (53)	8	3,000	87	66	53·1 (52·5–54)	35·5 (34·5–37)	66·8	—	—
55	Mt. Kabobo, 5° 8′ S., west side of Lake Tanganyika	10	5,200	?	?	58·9 (56–62)	41·4 (39–43)	70·3	13·5 (13–14)	22·9

Population.		Specimens examined.								
No.	Area and name.	No.	Mean altitude a.s.l. (ft.).	Temperature ° F. Max. (mean)	Temperature ° F. Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
	SOUTHERN TROPICAL AFRICA									
56	Kasai, S.W. Belgian Congo (*kasaica*)	13	2,000	88	64	52·5 (51–56)	35·1 (33–39)	66·9	12·0 (11–13)	22·9
57	N. Angola; Ndala Tando–Quicolungo	10	2,500	86	58	57·2 (54–59)	38·9 (35–42)	68·0	12·9 (12·5–14)	22·5
58	Angola highlands, Benguela plateau (*quanzae*)	27	5,500	83	45	61·8 (60–66)	43·9 (39–47)	69·4	13·0 (12·5–14·5)	21·0
59	Katanga–Upemba, S. Belgian Congo (*anderssoni*)	43	4,000	88	50	59·9 (57–63)	40·8 (36·5–44)	68·1	12·9 (12–14)	21·5
60	N. Rhodesia 3,500–5,500 ft. (*anderssoni*)	51	3,800	87	48	59·4 (56–62)	41·8 (39–45)	70·4	12·6 (12–14)	21·2
61	N. Rhodesia above 5,500 ft. (*anderssoni*)	18	5,800	80	41	61·0 (59–63)	42·5 (41–46)	69·8	—	—
62	S. Rhodesia (*anderssoni*)	19	4,500	83	43	59·3 (57–62)	39·8 (34–43)	67·9	12·9 (12–13·5)	21·7
63	Nyasaland, mainly *Brachystegia* country (*anderssoni*)	48	4,000	82	53	58·6 (55–62)	39·8 (34–43)	67·9	12·5 (11·5–13·5)	21·3
64	Nyasaland and Namuli mountain forests. (*stierlingi*)	23	6,000	76	46	58·5 (57–61)	41·0 (38·5–44)	70·0	13·1 (12–14)	22·4
65	Portuguese East Africa and Zululand, 15–28° S. (*tongensis*)	56	500	90	56	56·6 (55–60)	39·2 (35–43)	69·2	12·2 (11·5–13)	21·5
66	Kungwe and Ufipa highlands, east of Lake Tanganyika.	9	6,500	?	?	60·2 (58–62)	40·4 (38–43)	67·0	12·8 (12–14)	21·3
67	Songea, S.E. Tanganyika Territory (*niassae*)	17	4,000	82	54	57·7 (55–62)	38·9 (35–40)	67·4	—	—

Population.		Specimens examined								
			Mean altitude a.s.l.	Temperature ° F.						
No.	Area and name.	No.	(ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
68	Rungwe and Poroto Mts., S.W. Tanganyika Territory (*sarmenticia*)	16	7,000	72	45	58·6 (57–61)	40·2 (38–42)	68·6	12·7 (12–13·5)	21·7
69	Rest of S.W. Tanganyika Territory (*stierlingi*)	31	6,000	75	48	57·7 (56–60)	39·8 (37–43)	68·9	13·0 (11·5–14)	22·5
70	Nguru-Uluguru Mts., Tanganyika Territory (*stierlingi*)	20	5,000	79	53	56·4 (55–60)	37·8 (35–41)	67·0	12·8 (12–13·5)	22·7
71	W. Usambara Mts., N.E. Tanganyika Territory (*stierlingi*)	31	5,000	81	56	56·1 (53–58)	39·6 (35·5–42)	70·6	12·9 (12–13·5)	22·9
72	E. Usambara Mts., N.E. Tanganyika Territory (*stierlingi*)	8	3,000	82	59	54·4 (53–57)	37·8 (35·5–40)	69·5	13·0 (12·5–13·5)	23·7
	SOUTH AFRICA									
73	Interior 2,000 ft. upwards (*virens*)	28	4,000	82	38	62·1 (60–66)	46·6 (44–52)	75·0	13·9 (12·5–15)	22·4
74	Coastal Natal and Eastern Cape Province (*virens*)	45	1,000	82	49	59·6 (56–62)	45·1 (42–50)	75·5	13·4 (12–15)	22·5
75	Zululand and S. P.E.A. (*virens*)	25	1,000	84	51	59·6 (55–62)	44·8 (41–48)	75·2	13·4 (12–15)	22·6
76	O.F.S. and S.W. Transvaal (*pallida*)	35	4,000	87	35	59·3 (56–62)	47·0 (45–50)	79·2	12·6 (11–14)	21·2
77	S.W. Africa and N.W. Cape Province (*pallida*)	25	1,000	87	44	56·2 (54–58)	44·1 (42–48)	78·4	12·4 (11–13·5)	22·6
78	S.W. Cape Province (*capensis*)	26	500	80	46	59·2 (57–64)	46·5 (45–49)	78·6	13·6 (13–15)	23·0
79	Rest of Cape Province (*atmorii*)	52	1,500	82	43	60·1 (57–64)	46·0 (42–50)	76·7	13·5 (12–15)	22·5
80	Basutoland and borders (*atmorii*)	10	4,500	77	35	64·1 (62–66)	48·5 (46–50·5)	75·8	14·0 (13·5–14·5)	21·8

PART 2. GULF OF GUINEA

Island and name of bird[1]	Wing-length (mm.)		Tail-length (mm.)		Ratio 100 × tail / wing	Beak-length (mm.)		Ratio 100 × beak / wing
	Mean.	Range.	Mean.	Range.		Mean.	Range.	
GULF OF GUINEA								
Fernando Po, *brunnea* (1)[2]	—	(65)	—	(55)	82·7[2]	—	(13·5)	20·8
,, ,, *poensis* (12)	56·1	(54–59)	35·4	(33–38)	62·8	13·4	(12·5–14)	23·9
Principe, *leucophoea* (13)	68·3	(67–71)	47·7	(46–50)	69·8	14·9	(14–16)	21·8
,, *ficedulina* (6)	52·6[3]	(51–54)	37·7	(34–40)	71·7	13·5	(12·5–14·5)	25·7
São Tomé, *lugubris* (11)	74·4	(72–77)	46·0	(48–53)	61·8	15·9	(15–16·5)	21·4
,, ,, *feae* (16)	55·2[3]	(53–56)	37·1	(33–39)	67·2	12·7	(12–13·5)	23·1
Annobon, *griseovirescens* (10)	62·2	(59–64)	48·7	(46·5–51·5)	77·6	15·8	(14·5–17)	25·4

[1] Number of specimens examined is given in brackets. The name is taken from Sclater (1930) without prejudice to reconsideration.

[2] The only other known specimen is stated to have had wing 62, tail 50 (Salvadori, 1903). The wing/tail ratio is based on both specimens (see Note 28, Appendix 1).

[3] As most of the Principe birds available were females and the São Tomé were males or unsexed, the difference in mean wing-lengths on comparable series from the two islands would probably be less than the 2·6 mm. indicated.

PART 3. INDIAN OCEAN BIRDS

	Number of specimens examined.	Wing-length. mm.	Tail-length. mm.	Ratio 100 × tail / wing.	Beak-length. mm.	Ratio 100 × beak / wing.
MADAGASCAR AND OUTLIERS						
Madagascar below 4,000 ft.	55	54·8 (52–59)	37·3 (35–41)	67·6	13·5 (12–15)	23·7
Madagascar 4,000 ft. upwards	5	60·8 (59–63)	42·5 (39–44·5)	70·0	14·1 (13–15)	23·2
Gloriosa	6	56·8 (55–57·5)	39·5 (37–40)	69·5	13·9 (13–15)	24·6
Aldabra	4	52·1 (51–53)	38·2 (37–40)	73·3	11·5 (11–12)	22·0
Cosmoledo	1	56	36	64·3	14·0	25·0
Europa	8	55·9 (53–59)	42·4 (39–46)	75·8	—	—
COMORO ISLANDS						
Grand Comoro (*comorensis*)	1	52·5	35	66·6	12·5	23·8
,, ,, (*kirki*)	7	53·4 (52–54)	35·7 (35–36)	66·9	12·8 (11·5–13)	24·0
,, ,, (*mouroniensis*)	3	62·3 (60–64)	49 (45–52)	78·6	14·0	22·5
Mayotte	16	53 (52–54·5)	33·5 (32–35)	63·2	14·0 (13–15)	26·4
Anjouan	11	56·8 (54–58)	36·5 (33–38)	64·6	14·4 (14–15)	25·3

	Number of specimens examined.	Wing-length mm.	Tail-length. mm.	Ratio 100 × tail / wing.	Beak-length. mm.	Ratio 100 × beak / wing
SEYCHELLES						
Mahé	6	60·0 (58–61)	39·6 (39–41)	65·0	14·6 (13·5–15)	24·4
Marianne	6	59·4 (58–61)	41·8 (40–45)	70·5	14·7 (13·5–15)	24·7
OTHER ISLANDS						
Laccadives	3	55·7 (55–57)	40·0 (39·5–41)	71·8	12·8 (12·5–13)	23·0
Pemba	16	52·8 (50–55)	35·2 (33–37)	66·7	13·7 (12·5–14)	25·9
Socotra	11	56·1 (55–57)	40·3 (38–43)	71·8	13·5 (12–14)	24·0
MASCARENES						
Mauritius *mauritiana*	8	55·1 (54–56·5)	40·2 (38·5–42)	73·0	14·0 (13–14·5)	25·4
,, *curvirostris*	7	51·6 (51–53)	32·6 (31·5–35)	63·2	16·4 (15·5–17)	31·8
Réunion *borbonica*	13	55·1 (54–58)	40·2 (38–42)	73·0	13·5 (13–14)	24·5
,, *haesitata*	19	57·7 (56–60)	40·7 (36–43)	70·5	15·6 (14–17)	27·0

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